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THE DISTRIBUTION OF MATURE WESTERN ALASKAN AND KAMCHATKAN SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) IN THE NORTH PACIFIC OCEAN AND BERING SEA

by
Betty J. Landrum and Thomas A. Dark
Biological Laboratory, Bureau of Commercial Fisheries
Seattle, Washington, December 1965

ABSTRACT

Since 1955, meristic characters of sockeye salmon have been studied as a means of identifying and determining the distribution of salmon populations on the high seas. Certain *a priori* information (from tagging studies, catch statistics, etc.) has indicated that the primary contributors of sockeye salmon to the ocean areas investigated are streams of the Kamchatka Peninsula and western Alaska. Through discriminant function analysis, the proportions of mature western Alaskan and Kamchatka Peninsula salmon in annual collections of high seas samples have been determined. Sampling was conducted over broad areas of the North Pacific Ocean north of latitude 49°N and in the Bering Sea during the spring and summer of 1956–62.

The annual classification of samples has shown highly consistent dominance of salmon of one or the other continental type in certain ocean areas. Mature Kamchatkan sockeye salmon are numerically dominant in most samples taken from near the Kamchatka Peninsula eastward to approximately longitude 175°E in the Bering Sea and North Pacific Ocean. Western Alaskan sockeye salmon predominate in the Bering Sea from 175°E to 180° eastward to North America and in the North Pacific Ocean from 175°E to the western portion of the Gulf of Alaska. Intermingling of the continental stocks appears greatest in a longitudinal band between longitude 170°E and 180° in the North Pacific Ocean.

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INTRODUCTION

The Protocol to the International Convention for the High Seas Fisheries of the North Pacific Ocean has required information concerning the oceanic distribution of Asian and North American stocks of the species of Pacific salmon. Identification and classification of salmon populations taken on the high seas has been essential to the solution of the problem. In 1955 the U.S. Fish and Wildlife Service began a study of the morphology of Pacific salmon as a possible means of accomplishing such identification. These morpho-

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logical studies were continued through 1962 at the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington.

The political terms of reference and the biological rationale for the morphological studies of the sockeye salmon, *Oncorhynchus nerka* (Walbaum), were discussed extensively by Fukuhara *et al.* (1962). These authors, reasoning in part from the evidence of tagging and parasite studies and distance function analysis of morphological characters, tentatively assumed that most sockeye salmon in the waters north and south of the Aleutian Islands originated in western Alaskan or southwestern Kamchatkan streams. Their assumption was further supported by the observation that these areas are by far the largest producers of sockeye salmon. The same publication also described the results of using a discriminant function analysis (Fisher, 1936) of morphological data to estimate the proportions of the two continental populations in samples of sockeye salmon taken from the Bering Sea and North Pacific Ocean in 1956 and 1957. The initial analyses had satisfied, or evaluated the effects of not satisfying, most statistical and biological assumptions and had empirically established the mathematical model. It then became necessary to evaluate the precision of the point estimates computed by discriminant function analysis. Subsequently, for samples of sockeye salmon collected in 1958 and 1959, confidence intervals were developed for the point estimates of percentages of western Alaskan fish in each sample (Fukuhara, 1961).

In 1960, the return of approximately 35 million sockeye salmon to Bristol Bay resulted in one of the largest runs ever recorded. Bristol Bay sockeye salmon were expected, therefore, to have numerically dominated Asian sockeyes after June in the eastern North Pacific Ocean and Bering Sea. This expected dominance provided a unique circumstance for evaluating the efficacy of the discriminant function in classifying sockeye salmon on the high seas. With the expectation of a large predominance of Bristol Bay salmon over those from Asia, we reported the results of classification of samples taken on the high seas in the spring and summer of 1960 (Landrum and Dark, 1963).

After 1960 we reconsidered the basic assumption of discriminant function analysis that the individuals composing the samples to be classified belong to either of two populations. By 1961 the small accumulation of evidence on the origins of immature sockeye salmon in the oceans was insufficient to justify the continued inclusion of immature salmon in the classification procedures. The results of analyses of the collections of 1961 (Dark and Landrum, 1964) and 1962 (Landrum and Dark, 1964) were limited to mature salmon.

Sampling for the morphological studies of sockeye salmon was discontinued after the summer of 1962. Since that time we have examined particular aspects of the methodology and underlying assumptions of the classificatory procedures. Also, for high seas samples collected in 1956–60, we have recomputed the estimates of the proportion of each continental stock in the samples, based on mature salmon only.

This summary report presents a synthesis of the morphological studies and the results of classification of the 1956–62 collections of mature sockeye salmon. We have examined evidence supporting the underlying biological and statistical assumptions and have evaluated the possible effects of not satisfying these assumptions. These analyses provide a basis for determining the distribution of mature western Alaskan and Kamchatkan sockeye salmon in areas of the Bering Sea and North Pacific Ocean.

The samples of sockeye salmon were provided by several research groups. The Fisheries Research Board of Canada supplied samples from the streams and fisheries of British Columbia and from the Gulf of Alaska. The staff of the former Racial Sampling Program of the Seattle Biological Laboratory, Bureau of Commercial Fisheries, arranged, with the assistance of the Bureau's Alaska Regional Office, for inshore sampling in the streams and fisheries of Alaska and for obtaining samples from the Japanese mothership salmon fishery operating on the high seas. Sampling on the high seas by United States research vessels was conducted by the High Seas Salmon Research Unit.

All meristic counts and morphometric data on sockeye salmon specimens were obtained by the staff of the former Pacific Salmon Morphological Program of the Seattle Biological Laboratory, under the direction of Francis M. Fukuhara. Fukuhara, Sueto Murai, John J. LaLanne, and Arporna Sribhibhadh developed the classificatory procedures used to determine the origins of sockeye salmon on the high seas. We especially wish to thank Mr. Fukuhara who also provided valuable suggestions and advice throughout the analyses and preparation of this summary report.

Age determinations from scales which were required for the analyses of intra-area sources of variation were provided by the staff of the Seattle Laboratory's Age Analysis Unit, and Sueto Murai and Donald Worlund of the Biometrics Unit provided technical assistance and programmed the multivariate analyses of the International Business Machines Computer-650. The staff of the Biometrics Unit provided all computer analyses.

We also thank the following persons at the Bureau of Commercial Fisheries who read the manuscript and offered many helpful suggestions: Murray Amos, John J. LaLanne, Galen Maxfield, Robert Simpson, and

George Tanonaka.

SAMPLING

The sampling program was designed to obtain specimens from the principal sockeye salmon stocks of Asia and North America. The morphological information obtained from the salmon could then be applied to the problem of identifying the major stocks of sockeye salmon on the high seas.

INSHORE SAMPLING—WESTERN ALASKAN AND SOUTHWEST KAMCHATKAN POPULATIONS

Distinguishing Asian and North American sockeye salmon initially required definition of the morphological characteristics of sockeye salmon stocks of Asia and North America. Beginning in 1955, sampling included most major inshore fisheries and escapement areas of North America. Since Kamchatkan stream samples were not available, mature salmon were collected off the southwest coast of the Kamchatka Peninsula to establish the morphological characteristics of Asian sockeye salmon.

After determination of the morphological characteristics of the various stocks, samples of sockeye salmon taken on the high seas were classified by distance function analysis on the basis of the affinity of their meristic characteristics to those of samples from the various stocks (International North Pacific Fisheries Commission, 1959a, 1960a). Results of distance function analysis indicated that the high seas samples were mostly composed of salmon morphologically resembling either stocks from Bristol Bay streams in western Alaska or those collected off the southwest coast of the Kamchatka Peninsula.

Supplemental evidence supported the results of distance function analysis. Escapement and catch statistics had indicated that the rivers of western Alaska, principally those flowing into Bristol Bay, produced more sockeye salmon than any other North American area, and that in Asia the rivers producing major sockeye salmon stocks were confined to the Kamchatka Peninsula. Catch statistics available in the initial phase of the morphological studies had shown that western Kamchatkan stocks were numerically larger than those of eastern Kamchatkan streams (Semko, 1954; Taguchi, 1957). Statistics for more recent years, however, have indicated that the level of abundance of the eastern Kamchatkan (Kamchatka River) stocks was approaching that of the western Kamchatkan (Ozernaya River) stocks (INPFC, 1959b, 1960b, 1961).

On the basis of conclusions from the prior analyses that western Alaskan and Kamchatkan salmon were the principal stocks of interest, sampling was intensified

TABLE 1. Reference samples for the western Alaskan sockeye salmon population, 1956–62.

Area	Catch date	Number of fish
	1956	
Naknek River	7/6	87
" "	7/8	95
Egegik River	7/17	198
Ugashik River	7/23	187
Kvichak River	7/13	186
Wood River	7/11	187
Karluk River	6/22	187
" "	9/7	188
Red River	6/17	51
" "	6/18	131
Chignik River	7/16	23
" "	8/2	22
	1957	
Naknek River	7/3	93
" "	7/5	93
" "	7/11	56
" "	7/12	94
" "	7/21	49
" "	7/25	96
Egegik River	7/13	180
Ugashik River	7/19	184
Kvichak River	7/9	94
" "	7/10	90
Wood River	7/17	163
Karluk River	6/20	93
" "	8/21	105
" "	9/9	94
" "	9/17	117
Red River	6/21	193
Chignik River	7/25	42
" "	7/26	39
" "	7/27	57
" "	7/28	52
	1958	
Naknek River	7/9	93
" "	7/13	46
" "	7/14	27
" "	7/19	25
Egegik River	7/7	191
Ugashik River	7/16	161
" "	7/17	25
Kvichak River	7/10	131
" "	7/16	100
" "	7/24	245
Wood River	7/4	24
" "	7/5	169
Karluk River	6/26	121
" "	8/31	97
" "	9/2	24
Red River	6/24	59
" "	8/31	38
Chignik River	7/1	120
" "	7/31	95

Table 1. Continued.

Area	Catch date	Number of fish
	1959	
Naknek River	7/2	192
Egegik River	7/7	189
Ugashik River	7/11	192
Kvichak River	7/9	270
” ”	7/14	99
” ”	7/26	108
Wood River	6/29	162
Karluk River	6/24	120
Red River	6/25	118
Chignik River	6/29	119
” ”	8/2	77
	1960	
Naknek River	7/7	193
Egegik River	7/11	188
Ugashik River	7/14	188
Kvichak River	7/2	120
” ”	7/8	118
” ”	7/21	106
Wood River	7/7	181
Branch River	7/8	191
	1961	
Naknek River	7/13–18	75
Egegik River	7/10	179
Ugashik River	7/16	177
Kvichak River	6/29	110
” ”	7/8	111
” ”	7/11	123
Wood River	7/7	86
” ”	7/8	94
Branch River	7/26	116
	1962	
Naknek River	7/5	192
Egegik River	7/11	185
Ugashik River	7/18	185
Kvichak River	7/3	112
” ”	7/7	115
” ”	7/12	115
Wood River	7/4	190
Branch River	7/9	39

Table 2. Reference samples for Kamchatkan population, 1957–62.

Sampling location	Catch date	Number of fish
	1957	
50°52′N, 153°28′E	7/14	195
51°16′N, 153°39′E	7/14	194
52°08′N, 154°15′E	6/2	191
	1958	
51°08′N, 153°45′E	6/15	116
51°09′N, 153°40′E	6/25	119
50°49′N, 153°07′E	7/5	113
51°39′N, 154°10′E	7/15	119
	1959	
Ozernaya River	9/1	131
	1960	
52°37′N, 164°18′E	6/3	117
53°13′N, 164°44′E	6/18	101
49°22′N, 162°43′E	7/6	103
	1961	
49°21′N, 162°11′E	7/5	107
50°17′N, 162°48′E	6/28	96
	1962	
49°35′N, 166°26′E	6/12	113
49°22′N, 166°36′E	6/12	113

after 1957 in the streams of Bristol Bay and terminated in most other North American areas. The areas and dates of sampling and the numbers of sockeye salmon collected in major western Alaskan streams in 1956–62 are given in Table 1. Samples were collected at weirs and with beach seines on the main trunk of each river system. At each sampling site an attempt was made to obtain samples during the peak of the run. Since the peak of the run could only be known in retrospect, and because of the difficulties of collecting salmon in relatively inaccessible areas, samples were not always obtained at exactly the desired times and places.

Procurement of samples within the principal sockeye salmon streams of Kamchatka was generally impossible. In most years sampling of Asian stocks was restricted to waters near the coasts of Kamchatka. Most of these samples, caught in 4.8-inch-mesh gill nets (stretched measure), were taken by the Japanese fishery and some by Japanese research vessels (Table 2). Okhotsk Sea samples were collected in June and July of 1956, 1957, and 1958. In 1959 one sample was obtained late in the season (after the active period of fishing) from the Ozernaya River, a primary producer of sockeye salmon in southwest Kamchatka. From 1960–62 most samples of mature fish were collected from mid-June to early July off the southeast coast of the Kamchatka Peninsula. The timing of major sockeye salmon runs on the east and west coasts of the Kamchatka Peninsula (Sato, 1939) would imply that most fish available in the areas, and during the time of sampling, were from spawning areas of southwest Kamchatka.

High Seas Sampling

Research vessel and commercial fishery operations demonstrated a wide distribution of sockeye salmon throughout the Bering Sea and North Pacific Ocean

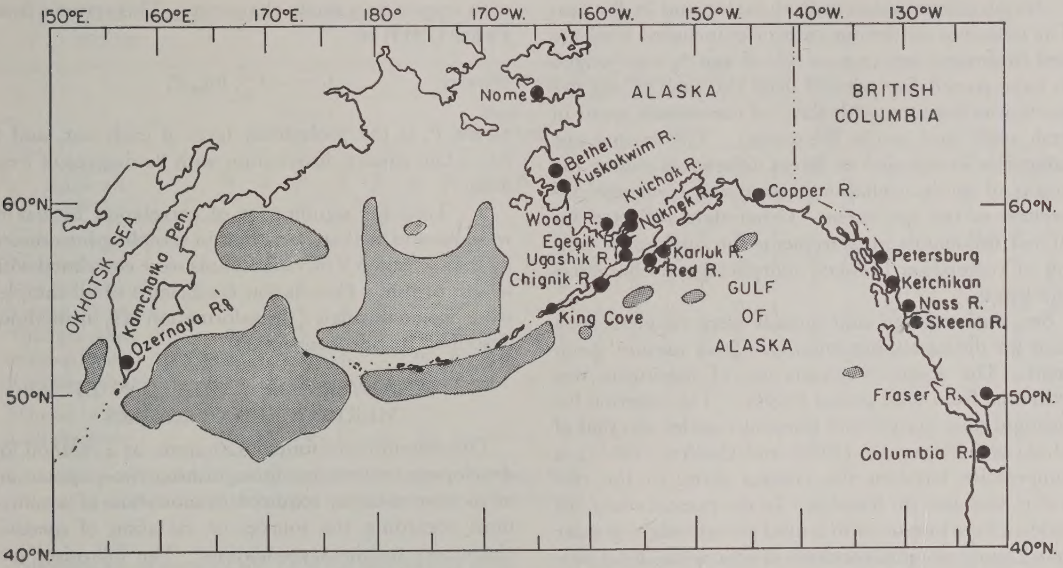

FIGURE 1. General areas of sampling of mature sockeye salmon in 1956–62.

during the spring and summer (INPFC, 1956). This extensive distribution and the limited availability of facilities and funds made it immediately apparent that the broad problem of identifying the continental origin of these salmon on the high seas required subdivision. One subdivision was time. Most sampling was undertaken in the months during which the Japanese mothership fishery operated—May through August. During this period, the presence of sockeye salmon of several life history stages in the waters sampled required a further subdivision. Since the principal objective of the Japanese fishing was mature salmon that could be expected to return for spawning in the year of their capture, sampling by the research vessels was modified to collect mainly mature sockeye salmon. The research vessels fished strings of nylon gill net with mesh sizes of 2½ inches, 3¼ inches, 4½ inches, and 5¼ inches (stretched measure). Since the net of 4½-inch mesh captured mature sockeye salmon most efficiently (INPFC, 1960a), more of this size was fished than of any other.

High seas samples of sockeye salmon to be classified to continent of origin were obtained from the Japanese mothership fishery and from Canadian, Japanese, and U.S. research vessels which fished over broad areas of the North Pacific Ocean and in the Bering and Okhotsk Seas. Figure 1 shows the general areas from which mature salmon were collected. Sampling was concentrated in the Bering Sea and in the North Pacific Ocean, generally north of latitude 50°N and west of longitude 170°W.

COLLECTION OF BIOLOGICAL DATA

Sockeye salmon samples taken on the high seas and from inshore areas in 1955–62 were sent to the laboratory where each fish was radiographed, and various morphometric measurements and counts were taken.

MERISTIC CHARACTERS

Seven meristic characters provided indices to distinguish Asian and North American stocks of sockeye salmon by discriminant function analysis: (1) number of scales along the lateral line; (2) number of vertebrae; (3) position of the first haemal arch; (4) number of ventral gill rakers; (5) total number of gill rakers; (6) number of pectoral fin rays; and (7) number of anal fin rays. The problems of selecting the characters and the criteria for their enumeration were reported by Fukuhara *et al.* (1962). Generally, more than one reader was employed in enumeration of the various osteological characters from radiographs; therefore, a close check of variability between readers was maintained to control individual bias and to assess the reliability of the criteria for counting. All counts of scales were made by one biologist. Both within- and between-counter variabilities were maintained at less than 2 percent.

OTHER BIOLOGICAL DATA

Sockeye salmon were categorized by total age, and by length of time spent in fresh water and in the sea. The notations for the age categories included total age and freshwater age (e.g., a fish of age 5_3 was judged to have passed five winters from the time of egg deposition to capture, with three of the winters spent in fresh water and two in the ocean). The various age categories were tested to detect differences among the means of meristic characters resulting from age differences of the specimens. Other data collected included fish-length measurements for subsequent testing of correlation between morphological characters and length.

Sex was recorded and gonads were weighed, as a basis for distinguishing immature from mature specimens. The stage of maturation of specimens was estimated from total gonad weight. The criterion for distinguishing mature and immature males was that of Ishida and Miyaguchi (1958) and Godfrey (1961); a compromise between the criteria given in the two studies was used for females. In the present study, all male sockeye salmon with a total gonad weight greater than 2 g and all female sockeye salmon with a total gonad weight greater than 15 g were considered mature.

All catch data and morphological data compiled at the laboratory were documented first on master data-recording forms and then on IBM punch cards. Major computational analyses were performed with the IBM-650 computer.

STATISTICAL TESTS

The following statistical tests were applied to meristic data from sockeye salmon:

1. Analysis of variance (F-test) was used to test the significance of differences among means of two or more distinct groups, such as fish of different brood years, sexes, etc.

2. Variance ratios were examined to test the assumption of equality of variances of two groups. The test is the ratio of the larger mean square over the smaller (Snedecor, 1956). Tabled percentiles of the F-distribution with appropriate degrees of freedom were employed to determine the significance of a ratio.

3. Bartlett's test was used to test for equality of variance of k normally distributed populations. The sampling distribution of the test statistic is approximately Chi square, with $(k-1)$ degrees of freedom, where:

$$M = (N-k) \log_e s_p^2 - \sum_{i=1}^{k} (n-1) \log_e s_i^2$$

and the expression s_p^2 equals the pooled variance, and s_i^2 are individual group variances (Snedecor, 1956).

4. A combination of probability test was used to evaluate the significance of a combined series of F-values obtained in testing differences between groups with respect to a single character. This statistic from Fisher (1944) is:

$$C = -2 \sum_{i=1}^{k} \log_e P_i$$

where P_i is the probability level of each test, and C has a Chi square distribution with $2n$ degrees of freedom.

5. Tests for significance of correlation bivariates were used to evaluate any bias in sampling introduced by gear selection if meristic counts were correlated with length of fish. Correlation coefficients of all samples were pooled through Z-transformation of r, by methods described by Snedecor (1956).

ANALYSES OF VARIATION IN MERISTIC CHARACTERS

The discriminant function analysis, as a method for developing criteria for distinguishing two populations of sockeye salmon, required examination of assumptions regarding the sources of variation of meristic characters within a population. The following sections discuss the intra-area sources of variation and the correlation of meristic characters with the length of the fish.

Analyses of Intra-Area Sources of Variation

Fukuhara *et al.* (1962), in selecting morphological characters to define Asian and North American continental morphotypes for discriminant function analysis, had assumed homogeneity within the variance components, such as sexes and year classes, in each population with respect to each character. The authors reported results of tests for homogeneity in the 1955–57 inshore samples. Estuarine samples, or those taken off the coast, could consist of heterogeneous stocks migrating to various streams of the adjacent continent; therefore only samples taken within North American streams were extensively analysed. First, for all characters, various components of each stream sample were tested for homogeneity; secondly, the test of combined probability was applied to test for general homogeneity of the components constituting the North American morphotype.

For the summary report, stream samples collected in 1958, 1959, and 1960 were analysed to provide information on any yearly or cyclic variation in the seven characters which were used in the discriminant function analysis. Variation within components of the stream samples could tentatively explain the annual variations in the percentages of correctly classified fish in samples from western Alaskan streams. Further analyses based on the 1961 and 1962 collections were discontinued as the materials would not contribute further significant information pertinent to the problem.

TABLE 3. Summary of tests for effects of intra-area sources of variation in western Alaskan sockeye salmon collected in 1955–60.

Meristic characters tested	Number of significant effects found annually for :																						
	Sexual dimorphism					Time of sampling						Freshwater age				Ocean age				Year class			
	'56	'57	'58	'59	'60	'55	'56	'57	'58	'59	'60	'55–'57	'57–'58	'58–'59	'59–'60	'55–'57	'57–'58	'58–'59	'59–'60	'55–'57	'55–'58	'56–'59	'56–'60
Scales on lateral line	1	1	1	1	2	0	0	1	0	0	0	0	1^a	0	0	1	0	0	1	0	4^a	5^b	3^b
Total vertebrae	0	1	0	1	1	0	0	0	2	0	0	1	1^a	0	0	1	0	0	0	0	2	4^b	2
First haemal arch	0	1	1	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0
Ventral gill rakers	1	1	1	0	0	0	0	0	2^a	1^a	0	0	0	1	0	1	0	0	0	0	1^a	3^b	2^b
Total gill rakers	0	1	0	0	0	0	0	0	2	1^a	0	0	0	2^a	0	1	0	1	0	0	2^a	4^b	4^b
Pectoral fin rays	2	0	3^a	0	1	0	0	0	1	1^a	0	1	2^a	0	0	0	0	2^a	0	1^a	1	0	0
Anal fin rays	2	0	3	2	1	0	0	1	3^b	0	0	2	4^b	1	0	1	0	0	0	1	6^b	4^a	6^b
Number of tests for each character	16	17	14	13	10	1	3	7	7	2	1	9	6	8	1	11	3	7	4	13	18	14	9

[a] Result of combination of probability test significant at 5-percent level.

[b] Result of combination of probability test significant at 1-percent level.

Subdivision of some of the 1958–60 samples by area, sample date, age group, and sex resulted in numbers within these components that were smaller than desirable for statistical analyses; for completeness of information, however, samples with 15 or more specimens in a component were used. Determination of freshwater age in sockeye salmon is subject to marked within- and between-reader variability (Cleaver, 1964). This variability must be considered as a possible source of error, particularly in tests of freshwater age effects on meristic characters.

Detailed data and results of each test of the 1958–60 samples are presented in Appendix Tables 1a to 5u. For ease of discussion and comparison, this material is summarized in Table 3, which includes results of the 1955–57 data reported earlier by Fukuhara *et al.* (1962). All tests were performed annually as samples became available. In the age-group tests, data from the new samples collected each year were added to those of previous years and are included in Table 3.

Effects of sexual dimorphism

Over the 6-year period, sexual dimorphism had a negligible effect on the means of meristic characters (Table 3). In the 1958 data, the combination of probabilities tests indicated possible sexual dimorphism in pectoral fin rays; in view of results from all years, however, this indication was not considered to be of serious consequence.

Effects of time of sampling

In both the 1958 and 1959 data, the means of some characters were significantly different among samples taken at different times within streams. Four of the 10 significant results in 1958 were attributable to differences between samples of 5_3- and 6_4-age[1] fish collected on June 26 and August 31 in the Karluk River (Appendix Tables 2b, 2f, and 2g). The Karluk River run has two peaks during the spawning migration, the first from early June to July 1 and the second from late July to mid-August. Our samples may reflect heterogeneity of two distinct stocks with different spawning times which correspond to the two peaks in the run. In 1959 all significant values occurred in samples taken on three different dates from the Kvichak River. Supplementary knowledge will be necessary to determine if the results actually were attributable to heterogeneity of samples taken from more than one breeding stock within a river.

Effects of freshwater age

Effects of freshwater age on meristic characters were apparent primarily in tests between samples collected in 1957 and 1958, although significant differences were also observed in the test of combined probabilities for total gill rakers from samples collected in 1958 and 1959. Over the entire period of collection, 1955–60, significant effects of freshwater age appeared in the combined probabilities tests of the scales along the lateral line, total vertebrae, total gill rakers, pectoral fin rays, and anal fin rays. Effects were not associated with unequal variances. These results are made questionable by difficulty in determining the freshwater age of sockeye salmon from scale readings.

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[1] The number refers to total age; subscript refers to freshwater age.

Effects of ocean age

In the tests of combined probabilities for ocean age effects, only the mean differences observed in pectoral fin ray counts from the 1958 and 1959 specimens were significant at the 5-percent level. These differences in means of pectoral fin ray counts were not attributable to unequal variances (Appendix Table 4m).

Effects of year class

Consistent year class differences occurred among the means of scales on the lateral line, ventral gill rakers, total gill rakers, and anal fin rays (Table 3). Means of neither total vertebrae nor pectoral fin rays appeared to be consistently affected by brood year, and tests of combined probabilities indicated no significant differences among means for the position of the first haemal arch.

Conclusions on intra-area variation

Earlier analyses of the 1955–57 data (Fukuhara *et al.*, 1962) had indicated that only the means of pectoral fin ray counts were affected by any considered intra-area source of variation. The current series of tests of the 1958–60 data have indicated that means of all characters, with the exception of the position of the first haemal arch, were affected to some degree by one or more within-stream sources of variation. The components of inshore samples were, therefore, heterogeneous, in varying degrees, with respect to the meristic characters. Significant differences among the means of different year classes became apparent only as more data for successive years were added. The additional data increased the degrees of freedom and thus the sensitivity of the analysis of variance tests. In evaluating these tests, it should be noted that the combination of probability test is highly sensitive to the presence of extremely low probability values in the series, leading to a disproportionate increase in type I errors (rejection of the null hypothesis when it should be accepted).

Aside from sampling variation and statistical considerations, other causes of observed differences in means of characters in the above analyses can only be hypothesized, because knowledge of the roles of genetics and environment in morphological development is so limited. It is possible that environmental conditions modified morphological characters in genetically homogeneous populations. Tåning (1944) and Seymour (1959) have shown experimentally the effects of different levels of temperature and oxygen content of the water on some morphological characters of fishes. Since such factors vary annually in nature, they could produce differences in development among year class groups within any particular stream. Another possibility, which may have accounted for some observed differences, is that two or more genetically distinct subpopulations within a river may have been included in a sample. The causes of observed variability in freshwater and ocean age groups are presently very speculative and may be related to genetic constitution, environment, errors in age determination, or some combination of these factors.

In view of the observed heterogeneity among components of the western Alaskan population, subsequent classification of high seas salmon into continental types could have been affected to some degree by the age composition of the samples rather than by the actual proportions of the two continental populations present. In view of the heterogeneity among various components of the populations, it became necessary to assume that sexes and the various age groups were randomly distributed in high seas samples. The possible effects of heterogeneity on the classificatory analysis are evaluated in a later section.

CORRELATION OF CHARACTERS WITH LENGTH

As most samples were collected with gear which was selective for fish size, possible correlation of characters with fish length was assessed. In earlier analyses of the 1955–57 inshore samples, Fukuhara *et al.* (1962) had found a negligible degree of variation in characters associated with variability in the length of the fish. They concluded that little bias in the distribution of characters would be introduced into the analyses by the various types of gear used to collect samples. By the use of similar statistical techniques, samples collected from various western Alaskan streams in 1958–60 were examined to evaluate the above conclusion further. Results are given in Table 4. The value of $100\ r^2$ is an approximation of the percentage of variability in each character associated with variability in fish length. The highest percentage calculated from the sample data was 1.6 percent for the number of scales on the lateral line. For the other characters, the percentage of variability associated with fish length was less than 1 percent. These additional observations substantiated the conclusion that bias introduced by gear selectivity would be negligible in the classificatory analyses.

UNDERLYING ASSUMPTIONS OF DISCRIMINANT FUNCTION ANALYSIS

One biological and two statistical assumptions underlie the application of discriminant function analysis: (1) the high seas salmon to be classified must be dichotomous, composed of only two populations, as the analysis specifies only two alternatives in the classification of samples obtained from the high seas; (2) the two populations to be classified must have com-

TABLE 4. Coefficients of correlation of meristic characters with fish length (mid-eye to hypural plate) in sockeye salmon, 1958–60.

Year and area of sampling	Number in sample	Scale along lateral line	Total vertebrae	First haemal arch	Ventral gill rakers	Total gill rakers	Pectoral fin rays	Anal fin rays
1958								
Chignik R.	120	.096	−.038	−.111	.108	.092	.024	.144
"	95	.083	−.117	−.072	.062	−.026	.125	−.055
Karluk R.	121	.036	.011	.037	.071	.106	.054	.083
"	97	−.029	−.055	.004	−.022	.061	.028	.172
Red R.	59	−.205	−.130	−.101	.051	.130	.219	.084
Naknek weir	93	.144	−.098	.081	.095	.097	−.050	.059
"	46	.289	.160	.174	−.028	.172	−.112	.152
"	25	.008	.065	−.079	−.234	−.053	−.105	.182
Egegik weir	191	.020	−.093	−.145	−.146	−.058	.008	.025
Ugashik weir	161	.070	−.089	−.054	.050	.036	−.059	−.097
Kvichak R.	131	.216[a]	.081	.040	−.048	−.012	.041	.027
"	100	.421[b]	.303[b]	.156	.113	.077	−.093	.104
"	245	.151[a]	.156[a]	.114	.089	.112	.026	.064
Wood R.	169	.031	−.045	.036	−.034	.028	.032	−.134
Cook Inlet	70	.259[a]	.133	.175	−.295[a]	.381[b]	−.125	.105
1959								
Fraser R.	117	.169	.080	−.052	.170	.120	.191[a]	−.033
Ozernaya R.	131	.062	.147	−.230[b]	−.021	−.065	.024	.046
Rivers Inlet	119	.325[b]	.238[a]	.217[a]	.170	.368[b]	.006	.010
Skeena R.	119	.212[a]	.126	.045	.332[b]	.369[b]	.081	.119
Nass R.	113	.075	.004	−.099	−.168	−.127	.161	.017
Chignik weir	119	.118	.039	−.110	.149	.210[a]	.249[b]	.024
"	77	.080	.003	−.069	−.086	−.163	−.066	−.017
Bear River	114	.172	.126	.014	.117	.101	.092	.147
Petersburg	113	.220[a]	.240[a]	.026	−.146	−.073	.012	.167
Karluk R.	120	.222[a]	.114	.009	.041	.063	−.040	.005
Red R.	118	−.088	.091	−.118	−.134	−.141	−.100	.015
Naknek weir	192	.206[b]	.123	.025	−.002	−.007	−.101	.125
Egegik weir	189	.000	.018	−.009	.052	.023	−.073	−.001
Ugashik weir	192	−.019	.012	.090	−.017	−.032	.048	−.002
Kvichak R.	270	.174[b]	.145	.060	−.036	−.006	−.070	.138
"	99	.056	.049	−.142	.123	.065	−.153	−.019
"	108	.057	.122	−.084	.007	−.032	−.088	.093
Wood R.	162	.191[a]	.039	−.006	−.045	.002	.166[a]	.090
Fish Creek weir	115	−.036	.061	−.021	.047	.110	−.024	−.067
Seldovia	37	−.009	.224	−.293	.054	.041	−.262	−.150
"	40	.396[a]	.154	.037	.307	.344[a]	.090	.037
Kuskokwim	42	.341[a]	.239	−.007	−.384[a]	−.079	.000	.103
"	50	.397[b]	.006	−.112	−.289[a]	−.040	.045	−.030
Copper R.	108	.360[b]	.349[b]	.114	.047	.190	.117	.103
Salmon Lake	56	.018	.043	−.120	−.144	−.106	.198	.299[a]
"	33	.105	.022	−.056	.314	.300	.155	−.134

Continued . . .

TABLE 4. Continued.

Year and area of sampling	Number in sample	Scale along lateral line	Total vertebrae	First haemal arch	Ventral gill rakers	Total gill rakers	Pectoral fin rays	Anal fin rays
1960								
Egegik	188	.036	−.079	.015	.108	.159[a]	.024	−.118
Ugashik	188	.178[a]	.156[a]	.000	−.012	.008	.060	.047
Naknek	193	.024	−.084	−.109	.073	.183[b]	.079	−.054
Kvichak 7/2	120	.181[a]	.213[a]	.216[a]	−.173	−.065	.033	.130
" 7/8	118	.049	−.026	−.004	.040	.102	.190[a]	.098
" 7/21	106	.182	.112	−.077	−.134	−.138	.004	−.001
Wood R.	181	.166[a]	.047	.094	.096	.143[a]	.064	−.036
Branch R.	191	.199[b]	.039	.070	.108	.161[a]	−.092	−.128
r^c	5,961	.128	.064	.002	.025	.061	.025	.032
$r^{2\ d}$		.016	.004	.000	.001	.004	.001	.001

[a] Significant at 5-percent level (null hypothesis : $\rho = 0$).

[b] Significant at 1-percent level.

[c] r is an estimated population correlation coefficient.

[d] 100 r^2 is the percentage of variation in the particular meristic character that can be explained in terms of length variation.

TABLE 5. Variances of meristic characters of sockeye salmon from western Alaskan and Kamchatkan reference areas and results of Bartlett's tests for homogeneity of variances, 1958–60 samples.

Year and area of sampling	Scales on lateral line	Total vertebrae	First haemal arch	Ventral gill rakers	Total gill rakers	Pectoral fin rays	Anal fin rays
1958							
Bristol Bay :							
Naknek R.	4.91	.97	.99	1.08	2.17	.30	.60
"	5.69	1.11	.87	.79	1.67	.40	.38
Egegik R.	3.38	.61	.72	1.01	1.89	.29	.43
Ugashik R.	3.24	.82	.61	.79	1.56	.30	.38
Kvichak R.	4.34	.92	.66	.92	1.94	.32	.42
"	5.78	1.05	.70	.92	2.01	.41	.50
"	4.92	.88	.93	1.07	2.26	.38	.45
Wood R.	3.29	.63	.73	.95	1.82	.31	.41
Kodiak I. :							
Karluk R.	3.85	.56	.70	.90	1.78	.27	.34
"	3.30	.73	1.04	1.13	2.61	.47	.36
Red R.	2.05	.53	.53	.79	1.82	.35	.50
"	6.79	.75	.85	1.16	1.92	.26	.44
Chignik	3.22	.66	.66	.77	1.58	.26	.38
"	2.68	.88	.75	.75	1.63	.28	.54
Kamchatkan :							
No. 1	4.19	1.19	.77	.70	1.34	.29	.35
No. 2	5.33	1.15	.76	1.20	2.38	.34	.48
No. 3	4.08	.98	.55	1.02	2.46	.28	.40
No. 4	4.78	.83	.80	.77	1.51	.22	.52
Character							
M values[a]	62.080[b]	55.462[b]	30.5196[c]	25.3826	33.2294[c]	32.6029[c]	23.0105

Continued . . .

Table 5. Continued.

Year and area of sampling	Scales on lateral line	Total vertebrae	First haemal arch	Ventral gill rakers	Total gill rakers	Pectoral fin rays	Anal fin rays
1959							
Bristol Bay:							
Naknek R.	3.86	.71	.71	.89	1.76	.29	.42
Egegik R.	2.92	.69	.71	.94	1.97	.32	.46
Ugashik R.	2.77	.44	.57	.85	2.11	.33	.33
Kvichak R.	4.37	.84	.78	.92	1.90	.35	.37
"	3.92	1.03	.76	.85	1.73	.42	.51
"	2.81	.84	.76	1.24	2.85	.29	.44
Wood R.	3.90	.89	.56	1.00	2.00	.34	.41
Kodiak I.:							
Karluk R.	2.83	.51	.72	1.00	2.08	.35	.47
Red R.	3.01	.76	.83	.91	1.93	.26	.42
Chignik	4.76	.87	.68	1.07	2.36	.30	.38
"	3.44	.91	.65	1.16	2.16	.35	.25
Ozernaya R.	4.52	.79	.84	.96	1.92	.34	.43
Character							
M value[d]	33.2515[b]	45.0485[b]	14.0114	9.2372	12.6893	10.0297	19.1899
1960							
Bristol Bay:							
Naknek R.	4.90	.92	.92	.83	1.79	.32	.46
Egegik R.	2.16	.48	.65	.79	1.71	.27	.41
Ugashik R.	3.20	.55	.60	.91	1.71	.30	.41
Kvichak R.	3.85	.87	.72	1.07	2.20	.39	.47
"	3.51	.66	.61	.95	1.92	.37	.46
"	4.09	.61	.67	.86	1.98	.37	.45
Wood R.	3.79	.72	.59	1.03	2.12	.29	.39
Branch R.	2.96	.61	.59	.85	1.64	.32	.49
Kamchatkan:							
No. 1	3.30	.60	.75	1.15	2.58	.36	.39
No. 2	4.44	.86	1.05	1.02	2.43	.29	.40
No. 3	4.12	.82	.84	.97	2.17	.33	.49
Character							
M values[e]	41.0906[b]	35.7971[b]	29.7170[c]	10.0860	16.3114	10.0560	5.7982
M values							
1958–60[f]	146.7172[b]	152.7728[b]	76.4759[b]	45.2380	63.7092[b]	53.1801	50.8310

[a] $\chi^2_{.95}$ with (18–1) d. f. = 27.59.

[b] significant at 1-percent level.

[c] significant at 5-percent level.

[d] $\chi^2_{.95}$ with (12–1) d. f. = 19.68.

[e] $\chi^2_{.95}$ with (11–1) d. f. = 18.31.

[f] $\chi^2_{.95}$ with (41–1) d. f. = 55.76.

mon variance-covariance for all characters; and (3) the characters must be normally distributed. Evidence supporting these assumptions is discussed in the following paragraphs.

Dichotomous Population of High Seas Salmon

The discriminant function analysis which has been used in the morphological studies assumes that most sockeye salmon taken in high seas samples are members of either the major western Alaskan or Kamchatkan populations. In other words, only two alternatives are specified by the classification procedures, and salmon from extraneous populations will be classified as either Kamchatkan or western Alaskan salmon, depending upon their morphological characteristics. The rationale for the assumption of a dichotomous high seas population was fully developed by Fukuhara *et al.* (1962), and for mature salmon further information has substantiated the assumption. Also, elements of time and distance to spawning areas during the period of sampling (May–August) restricted the possible origin of the great majority of mature salmon to two areas, namely, the Kamchatka Peninsula and western Alaska. Lack of knowledge of the factors influencing the distribution of immature salmon and of supplementary evidence from other sources, however, precludes application of a similar rationale to immature salmon. Consequently, in this report, only salmon that were mature (as indicated by gonad weights) and therefore would have spawned during the year of capture, were used in determining the high seas distribution of Kamchatkan and western Alaskan sockeye.

Common Variance-Covariance

Discriminant function analysis assumes common variances-covariances of the morphological characters between two populations. Data from the 1956 reference samples for the western Alaskan and Kamchatkan populations (Fukuhara *et al.*, 1962) indicated some heterogeneity of variances in the number of scales on the lateral line, total number of vertebrae, and total number of gill rakers on the first left gill arch. Since the contribution of these characters to the separation of population means, however, appeared to be more advantageous than any possible reduction in the efficiency of the discriminant function, all three characters were retained in the function. Because homogeneity of variances alone would have been insufficient to ensure equality of the covariance matrices of the two populations, the effect of not satisfying the assumption of homogeneity of variances was tested empirically by using the 1956 discriminant function to classify Kamchatkan and western Alaskan samples collected in the following year. The percentage of correctly classified individuals in the 1957 western Alaskan and Kamchatkan reference samples closely approximated the theoretically expected percentages of correct classification, and demonstrated that the effect of heterogeneity of variances was not appreciable.

For the present report, stream samples taken in the succeeding years, 1958–60, were tested for homogeneity of variances. Those tests provided a basis for further assessment of the effect of any heterogeneity in morphological characters collected after 1957. Table 5 presents the data and results of Bartlett's test for homogeneity of variance and a combined result for the collections made in 1958–60.

Results of Bartlett's tests for 1958–60 substantiated those for 1956. Variances were unequal for the number of scales on the lateral line, total vertebrae, total gill rakers, and in the 1958 and 1960 samples, for the first haemal arch. Results were significant in the 1958 samples of pectoral fin rays, but the M value of 53.18 for the combined test on all the data for this character was not significant at the 5-percent level. The greatest disparity (scales on the lateral line), however, was only on the order of the largest variance, being three times as great as the smallest. Empirically, this magnitude was considered of small consequence, since the function derived from the meristic characters correctly classified samples from known populations in accordance with the theoretical expectation of correct classification. In evaluating the evidence for heterogeneity of variance, it should also be recognized that Bartlett's test is affected by any kurtosis and skewness in distributional curves. Verification of the source of the observed discrepancies in variances, therefore, will require more exacting examination.

Normal Distribution of Characters

In the absence of a good test of normality in small samples (Fisher, 1944; Cochran, 1947) the frequency distributions of counts for individual characters for specimens collected in 1958–60 were examined for departures from normality. No discernible deviations from normality occurred, and the curves approximated those obtained from the 1956 collections by Fukuhara *et al.* (1962). The 1960 distributional curves are shown in Appendix Figures 6a to 6g. Distribution curves do not provide proof of normality of the joint distribution of characters of continental stocks. Since no obvious deviations from normality were observed, however, rejection of the assumption was not indicated. Except in instances of radical departures from normality, violation of the assumption is generally recognized to have little effect on the results.

CLASSIFICATORY PROCEDURES

The determination of the proportions of Kamchatkan and western Alaskan salmon in samples from the high seas involves several classificatory procedures. The first is development of a discriminant function which will efficiently classify samples from the two continental populations. The second is to establish the probabilities of misclassifying fish from each population. Then the point estimates of the proportions of western Alaskan fish in each high seas sample are determined. A 90-percent confidence interval is calculated for each point estimate.

Discriminant Function

The discriminant function developed from the meristic characters of western Alaskan and Kamchatkan salmon collected in 1956 (Fukuhara *et al.*, 1962) was employed for classification of all collections taken in 1956–62. Its discriminating ability was essentially constant, as was shown by yearly classification of inshore samples from western Alaskan streams. The average percentage of correctly classified fish in the 1957–62 western Alaskan population varied little from the average percentage of correctly classified salmon in the original 1956 western Alaskan samples or from the theoretically expected proportion of correct classification as calculated by Fukuhara *et al.* (1962). This agreement indicated that the variation in individual characters from year to year was insufficient to effect radical changes in the efficacy of the 1956 discriminant function in correctly classifying samples collected in other years. To evaluate the efficacy of the 1956 function further, it was compared with new functions derived annually from data obtained from reference samples of western Alaskan and Kamchatkan salmon collected each year from 1957 to 1960. These functions gave percentages of correctly classified fish in inshore samples, which were used as reference samples, that were comparable to those attained with the original 1956 function.

Errors of Misclassification

Estimates of the probabilities of misclassifying salmon from each population must be established during the classificatory procedures. The errors of misclassification inherent in the discriminant function analysis are caused by an overlap in the distributions of counts of meristic characters of Kamchatkan and western Alaskan salmon. By observing the percentages of fish misclassified in population reference samples correction factors have been devised to estimate more accurately the proportions of each population present in high seas samples.

The percentages of misclassified fish in samples collected from western Alaskan rivers vary. To estimate the average error of misclassification of the western Alaskan population, the observed percentages of misclassified specimens in the different reference samples are weighted by the relative abundance of the contributing stocks as determined from escapement estimates. This weighting assumes that these stocks occur in high seas samples in the same proportions. Because the discriminant function effects very little separation among the various western Alaskan stocks, specimens from these stocks in a mixed sample cannot be identified; therefore, no rigorous test of the assumption has been devised. Since contrary evidence is lacking, however, the weighting technique appears to provide the best available estimate of the average error of misclassification of the western Alaskan population.

The misclassified fish in Kamchatkan reference samples have not been similarly weighted. Lack of any information regarding the precise origin of stocks comprising the offshore samples which have been used for estimating the errors of misclassification of the Kamchatkan population preclude weighting by the relative abundance of any contributing stocks.

Tables 6 through 11 present the computations of the estimated probabilities of misclassifying western Alaskan and Kamchatkan sockeye salmon on the high seas in 1956–62. Essentially, these tables are those presented in Fukuhara *et al.* (1962), and in the International North Pacific Fisheries Commission's annual reports for the years 1960 through 1963 (INPFC, 1961–1964). Elimination of a few immature specimens from the original samples used in some of the above reports caused only slight changes in some average errors of misclassification for Kamchatkan fish. Fukuhara *et al.* (1962) pooled the escapement estimates for 1956 and 1957 in the western Alaskan streams (Table 6) to obtain relative abundance estimates for the two years. These figures were then used to calculate the average error of misclassification of western Alaskan fish which was applied in classification of the 1956 and 1957 high seas samples.

Samples from the Chignik, Red, and Karluk Rivers, on the Pacific Ocean side of the Alaska Peninsula, were included in estimates of the probability of misclassifying western Alaskan sockeye salmon on the high seas in 1956–59. After 1959, sampling in these streams was discontinued owing to lack of evidence that the rivers contributed any sizeable number of fish to the high seas areas considered. The Branch River escapement was considered a significant contributor in the Bristol Bay area in 1960 because it exceeded the escapements of the Naknek and Wood Rivers. The Branch River was henceforth included in the complex of Bristol Bay rivers for calculation of the average error of misclassification for 1960–62.

The average error of misclassification of western

Alaskan sockeye (P_a) varied from about 18 to 24 percent from 1956 to 1962. Individual river samples had errors of misclassification of 11 to 58 percent. The highest percentage of misclassification was in the 1960 sample from the Branch River. Samples from Branch River misclassified by 57 percent in 1961 and 33 percent in 1962. Since the 1962 sample contained only 39 specimens, its adequacy was questionable. The Kvichak River, with only 13 to 23 percent misclassification, was generally the dominant system; it produced an average of about 45 percent of the total Bristol Bay sockeye salmon runs in the years of sampling.

For estimating the probability of misclassification of Kamchatkan salmon on the high seas in 1956–58, samples collected in the Okhotsk Sea were considered representative of the major southwest Kamchatkan stream stocks. An inshore sample was obtained from the Ozernaya River in 1959. Although the sample was taken on September 1, after the period of active fishing in this river, the lack of more desirable Kamchatkan inshore samples necessitated use of the Ozer-

TABLE 6. Average errors of misclassification in 1956–57 sockeye salmon samples, and errors from western Alaska weighted according to the relative abundance of the contributing stocks.

River	Escapement in 1956 and 1957 (millions)	Relative abundance	Observed percentage of misclassification	Weighted value
Naknek	2.406	.1212	21.6	2.6158
Egegik	1.493	.0752	18.9	1.4213
Ugashik	.636	.0320	22.3	.7136
Kvichak	12.407	.6247	15.2	9.4954
Wood	1.070	.0539	40.8	2.1991
Karluk	.357	.0180	22.5	.4050
Red	.225	.0113	12.9	.1458
Chignik	1.265	.0637	12.6	.8026
Total	19.859	1.0000	—	17.7988

Average errors of misclassification:

Western Alaskan population (P_a) = 17.7988 percent

Kamchatkan population

$$(P_b) = \frac{20.62+25.64+25.13}{3} = 23.7966 \text{ percent}$$

TABLE 7. Average errors of misclassification in 1958 sockeye salmon samples, and errors from western Alaska weighted according to the relative abundance of the contributing stocks.

River	Escapement in 1958 (millions)	Relative abundance	Observed percentage of misclassification	Weighted value
Naknek	.2781	.0873	35.1	3.0642
Egegik	.2463	.0773	15.7	1.2136
Ugashik	.2795	.0878	13.4	1.1765
Kvichak	.5348	.1680	18.9	3.1752
Wood	.9618	.3020	25.4	7.6708
Karluk	.4636	.1456	29.3	4.2661
Red	.0948	.0298	20.6	.6139
Chignik	.3253	.1022	13.9	1.4206
Total	3.1842	1.0000	—	22.6009

Average errors of misclassification:

Western Alaskan population (P_a) = 22.6009 percent

Kamchatkan population

$$(P_b) = \frac{27.43+32.77+18.97+36.13}{4} = 28.8250 \text{ percent}$$

TABLE 8. Average errors of misclassification in 1959 sockeye salmon samples, and errors from western Alaska weighted according to the relative abundance of the contributing stocks.

River	Escapement in 1959 (millions)	Relative abundance	Observed percentage of misclassification	Weighted value
Naknek	2.2326	.3052	28.6	8.7287
Egegik	1.0724	.1466	14.3	2.0964
Ugashik	.2192	.0300	14.1	.4230
Kvichak	.6697	.0915	22.6	2.0679
Wood	2.2107	.3022	23.6	7.1319
Karluk	.4442	.0607	32.5	1.9728
Red	.0842	.0115	16.9	.1944
Chignik	.3826	.0523	18.0	.9414
Total	7.3156	1.0000	—	23.5565

Average errors of misclassification:

Western Alaskan population (P_a) = 23.5565 percent.

Ozernaya River population (P_b) = 36.6412 percent.

TABLE 9. Average errors of misclassification in 1960 sockeye salmon samples, and errors from western Alaska weighted according to the relative abundance of the contributing stocks.

River	Escapement in 1960 (millions)	Relative abundance	Observed percentage of misclassification	Weighted value
Naknek	.828	.0380	38.3	1.4554
Egegik	1.798	.0824	29.1	2.3978
Ugashik	2.304	.1056	20.7	2.1859
Kvichak	14.630	.6706	16.6	11.1320
Wood	1.016	.0466	28.2	1.3141
Branch	1.240	.0568	57.6	3.2717
Total	21.816	1.0000	—	21.7569

Average errors of misclassification:

Western Alaskan population (P_a) = 21.7569 percent

Kamchatkan population

$$(P_b) = \frac{22.77+22.22+35.92}{3} = 26.9700 \text{ percent}$$

TABLE 10. Average errors of misclassification in 1961 sockeye salmon samples, and errors from western Alaska weighted according to the relative abundance of the contributing stocks.

River	Escapement in 1961 (millions)	Relative abundance	Observed percentage of misclassification	Weighted value
Naknek	.351	.0620	26.7	1.6554
Egegik	.702	.1240	20.1	2.4924
Ugashik	.349	.0617	21.5	1.3266
Kvichak	3.706	.6549	13.4	8.7757
Wood	.461	.0815	22.8	1.8582
Branch	.090	.0159	56.9	.9047
Total	5.659	1.0000	—	17.0130

Average errors of misclassification:

Western Alaskan population (P_a) = 17.0130 percent

Kamchatkan population

$$(P_b) = \frac{37.3832+36.4583}{2} = 36.9207 \text{ percent}$$

TABLE 11. Average errors of misclassification in 1962 sockeye salmon samples, and errors from western Alaska weighted according to the relative abundance of the contributing stocks.

River	Escapement in 1962 (millions)	Relative abundance	Observed percentage of misclassification	Weighted value
Naknek	.723	.1303	21.4	2.78842
Egegik	1.027	.1851	21.1	3.90561
Ugashik	.255	.0460	10.8	.49680
Kvichak	2.580	.4650	12.9	5.99850
Wood	.873	.1574	34.7	5.46178
Branch	.090	.0162	33.3	.53946
Total	5.548	1.0000	—	19.19057

Average errors of misclassification:

Western Alaskan population (P_a) = 19.1906 percent

Kamchatkan population

$$(P_b) = \frac{37.1681+33.6283}{2} = 35.3982 \text{ percent}$$

naya River sample to estimate the probability of misclassifying Kamchatkan salmon taken on the high seas in that year. In 1960, because of the absence of Kamchatkan stream samples or a Japanese fishery in the Okhotsk Sea, three samples taken off the southeast coast of Kamchatka on June 3, June 18, and July 6 provided an estimate of the average error of misclassification of Kamchatkan salmon. In both 1961 and 1962, two samples were selected from similar areas for use as reference samples. These sample selections were based on maturity of the specimens and on the time-space relation of the samples to Kamchatkan streams. More explicitly, the route rate and the precise timing of the spawning migration influence the distribution of mature salmon on the high seas; i.e., the distance to the spawning ground must not be so great that the members of a particular stock fail to arrive during the spawning period characteristic of the stock. Most of the Kamchatkan reference samples were collected from mid-June to early July near the Kamchatka Peninsula. Because the Bristol Bay runs peak by mid-July, it is very improbable that mature Bristol Bay salmon would have been near Kamchatka. If a migration rate of 30 miles per day is assumed (Hartt, 1962), salmon so far from their natal streams in Bristol Bay would have arrived too late for normal spawning.

The average error of misclassification of Kamchatkan sockeye salmon varied from about 24 percent in the Okhotsk Sea samples to about 37 percent in the reference samples taken off the southeast coast of Kamchatka. The error of misclassification of the Ozernaya River sample collected in 1959 was also about 37 percent. If it is assumed that the latter sample was representative of the Ozernaya River sockeye stock, then possibly the earlier Okhotsk Sea samples were not dominated by elements of the same stock. At the same time, the 1961 reference samples collected off the southeast coast of Kamchatka may have consisted entirely of Ozernaya River fish. The possibility of annual variation of the observed magnitude, however, cannot be entirely dismissed. These observations emphasize the need for more adequate sampling of stocks of Asian sockeye salmon.

COMPUTATION OF POINT ESTIMATES

The observed errors of misclassification in the two continental populations theoretically correspond to the probabilities of misclassifying these populations when they are found on the high seas. The classification of high seas samples is not only biased by the errors of misclassification, but also by the true relative abundance of the two populations. If a sample consists of fish from only one population then the error of misclassification is maximum. When fish from both populations are present, the errors of misclassification compensate and the bias is reduced. To correct for the errors of misclassification and the true relative abundance, the following factor was applied to observed numbers of salmon classified as western Alaskan morphotype in each high seas sample:

$$\frac{N_a}{N} = \frac{P_b - \left(\frac{R_a}{N}\right)}{P_a + P_b - 1}$$

where: N = sample size

N_a = corrected number of western Alaskan salmon in the sample

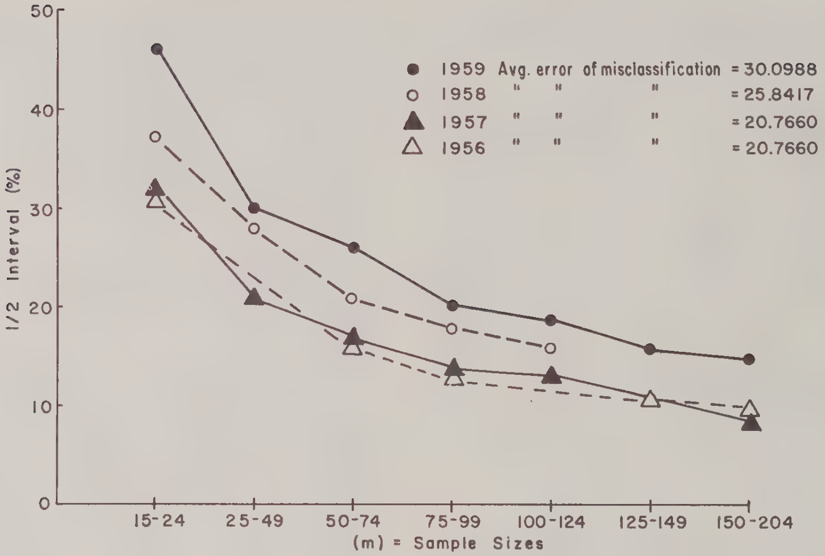

FIGURE 2. One-half confidence intervals for point estimates of western Alaskan sockeye salmon in high seas samples of various sizes (from Fukuhara, 1961).

R_a=number of fish classified as western Alaskan type

P_a=probability of misclassifying western Alaskan fish as Kamchatkan type

P_b=probability of misclassifying Kamchatkan fish as western Alaskan type.

The values, P_a and P_b, used in this formula were obtained from the weighted western Alaskan (P_a) and unweighted Kamchatkan (P_b) average errors of misclassification estimated from the annual reference samples from the continental populations. Then the corrected percentage of western Alaskan sockeye salmon in each sample was obtained from the expression 100 N_a/N.

CONFIDENCE INTERVALS

Additional information concerning high seas classifications has been provided by confidence intervals (Worlund and Fredin, 1962) constructed around the point estimates of the proportion of western Alaskan sockeye salmon in high seas samples. The confidence intervals reflect the variance of the estimates and also indicate the sample size necessary to obtain desirable precision in point estimates.

Figure 2, taken from Fukuhara (1961), illustrates that with errors of misclassification of about 20–30 percent, the length of the confidence interval rapidly decreases with increased sample size until sample sizes approach 100 to 150 specimens. With sample sizes of 100 to 150 fish, the width of the confidence interval decreases more slowly, and in samples of more than 150 fish further change in the width of the confidence interval is small. In samples larger than 150 fish, the limiting factor in attaining greater precision is not sample size so much as the error of misclassification in the discriminant function. The estimates of the error have fluctuated yearly; consequently an increase in the average percentage of misclassification results in an increase in the sample sizes necessary to maintain the same widths of confidence intervals.

HIGH SEAS DISTRIBUTION OF SOCKEYE SALMON

The distributions of Kamchatkan and western Alaskan sockeye salmon populations on the high seas, as shown by the classification of samples, are presented by the year of collection, 1956–62. Generally, samples from the North Pacific Ocean and Bering Sea are discussed separately to show differences within these areas during the migrations of populations toward their natal streams. Consecutively numbered samples are arranged in tables by collection location from western to eastern longitudes, and are plotted in appropriate figures for each sampling year. The tables present the percentages of fish classified as Kamchatkan and western Alaskan morphotypes in each sample, the corresponding point estimates of the corrected percentages

TABLE 12. Classification of mature sockeye salmon: 1956 high seas samples.

		Position			Percentage classified			
Sample number	Sampling date	Latitude	Longitude	Size of sample	Kamchatkan type	Western Alaskan type	Corrected percent western Alaskan type	90 percent confidence limits[1]
1	7/13	51°22′N	153°51′E	69	73.91	26.09	3.9	0–19
2	6/21	51°49′N	154°06′E	132	78.03	21.97	0.0	0–10
3	7/6	51°55′N	154°13′E	167	76.05	23.95	0.3	0–10
4	6/28	52°08′N	154°32′E	186	79.03	20.97	0.0	0–9
5	8/5	51°40′N	159°50′E	122	75.41	24.59	1.4	0–12
6	7/25	51°04′N	163°08′E	149	75.17	24.83	1.8	0–12
7	6/5	52°08′N	170°52′E	82	39.02	60.98	63.7	48–79
8	6/15	51°40′N	170°58′E	162	53.09	46.91	39.6	29–51
9	7/6	49°35′N	171°46′E	123	75.61	24.39	1.0	0–12
10	6/15	51°56′N	172°30′E	89	49.44	50.56	45.8	31–61
11	6/5	51°38′N	173°38′E	73	53.42	46.58	39.0	23–55
12	6/16	50°00′N	175°00′E	26	61.54	38.46	25.1	0–52
13	5/28	50°22′N	176°04′E	80	25.00	75.00	87.7	74–100
14	5/25	50°30′N	176°07′E	39	43.59	56.41	55.8	33–78
15	6/26	53°20′N	178°14′E	172	36.63	63.37	67.8	58–78
16	6/20	56°00′N	170°00′W	297	23.57	76.43	90.1	83–97

[1] Confidence interval truncated at 0 and 100 percent.

of western Alaskan morphotype, and the computed 90 percent confidence limits. For completeness of geographic coverage, samples containing as few as 15 fish have been included with reservations regarding the accuracy of the point estimates computed for small samples; any lack of precision is reflected by the size of the confidence intervals.

1956 SAMPLES

Limited high seas sampling in 1956 (16 samples of mature salmon) restricted determination of the distribution of continental stocks on the high seas in that year. Results of classifying the 1956 samples are presented in Table 12. In May and June, 11 samples of mature salmon were available for analysis (Fig. 3); two samples had been collected in the Bering Sea, seven in the western North Pacific Ocean, and two in the Okhotsk Sea. In July and August, only five samples were available from the North Pacific Ocean and Okhotsk Sea. The majority of the samples had been

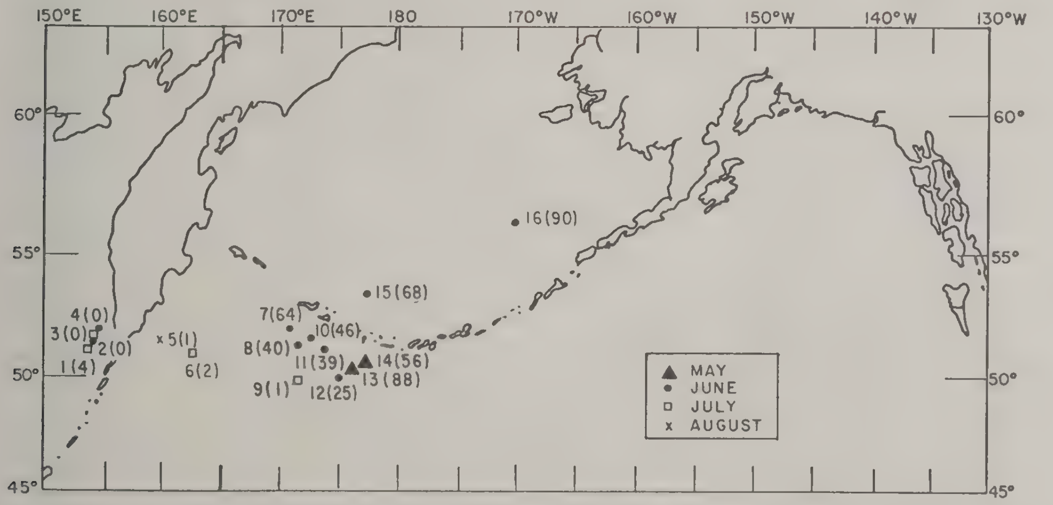

FIGURE 3. Percentages of mature sockeye salmon classified as western Alaskan type in samples collected in May-August 1956. (First number at each locality is sample number; number in parentheses shows percentage western Alaskan type.)

TABLE 13. Classification of mature sockeye salmon: 1957 high seas samples.

Sample number	Sampling date	Position		Size of sample	Percentage classified		Corrected percent western Alaskan type	90 percent confidence limits[1]
		Latitude	Longitude		Kamchatkan type	Western Alaskan type		
1	7/4	50°52′N	153°28′E	195	74.36	25.64	3.2	0–12
2	7/14	51°16′N	153°39′E	194	79.38	20.62	0.0	0–9
3	6/24	52°08′N	154°15′E	191	74.87	25.13	2.3	0–11
4	7/10	49°14′N	158°11′E	60	71.67	28.33	7.8	0–24
5	7/14	49°02′N	158°20′E	57	70.18	29.82	10.3	0–27
6	7/15	48°57′N	158°30′E	45	73.33	26.67	4.9	0–24
7	7/24	51°13′N	159°45′E	84	71.43	28.57	8.2	0–22
8	7/22	51°22′N	160°15′E	100	64.00	36.00	20.9	7–34
9	7/5	51°28′N	161°15′E	49	63.26	36.74	22.1	3–42
10	7/10	52°36′N	161°21′E	104	72.12	27.88	7.0	0–19
11	7/20	51°39′N	161°40′E	80	66.25	33.75	17.0	2–32
12	6/30	52°28′N	161°42′E	90	62.22	37.78	23.9	10–38
13	7/1	51°39′N	162°16′E	47	74.47	25.53	3.0	0–21
14	6/20	52°33′N	166°04′E	86	77.91	22.09	0.0	0–13
15	7/15	58°12′N	166°48′E	33	57.58	42.42	31.9	8–56
16	5/21	48°08′N	167°40′E	53	71.70	28.30	7.7	0–25
17	5/31	49°02′N	167°25′E	53	66.04	33.96	17.4	0–36
18	7/13	57°26′N	167°27′E	17	76.47	23.53	0.0	0–29
19	6/28	51°40′N	167°27′E	26	80.77	19.23	0.0	0–24
20	5/25	52°31′N	168°27′E	42	59.52	40.48	28.6	7–50
21	5/21	51°15′N	169°02′E	36	55.56	44.44	35.3	12–59
22	7/12	57°02′N	169°11′E	28	67.86	32.14	14.3	0–39
23	5/27	51°28′N	169°55′E	39	51.28	48.72	42.7	20–65
24	7/6	54°51′N	170°24′E	18	61.11	38.89	25.8	0–58
25	6/20	53°00′N	175°00′E	19	63.16	36.84	22.3	0–54
26	6/10	50°00′N	175°00′E	25	64.00	36.00	20.9	0–48
27	6/12	50°00′N	175°00′E	20	40.00	60.00	62.0	31–93
28	7/1	58°10′N	177°17′E	37	37.84	62.16	65.7	43–88
29	6/27	58°15′N	179°10′E	54	29.63	70.37	79.7	62–97
30	6/22	53°00′N	180°	37	24.32	75.68	88.8	69–100
31	6/15	56°00′N	175°00′W	191	20.42	79.58	95.5	87–100
32	6/30	56°00′N	175°00′W	37	29.73	70.27	79.6	58–100
33	6/8	53°00′N	175°00′W	46	17.39	82.61	100.0	84–100
34	6/9	53°00′N	175°00′W	51	23.53	76.47	90.2	74–100
35	6/10	53°00′N	175°00′W	43	18.60	81.40	98.6	82–100
36	6/17	56°00′N	173°00′W	145	20.69	79.31	95.0	86–100
37	6/18	56°00′N	170°00′W	85	22.35	77.65	92.2	80–100
38	6/19	56°00′N	170°00′W	63	12.70	87.30	100.0	86–100
39	6/21	56°00′N	168°00′W	61	26.23	73.77	85.6	70–100
40	6/22	56°00′N	168′00′W	85	34.12	65.88	72.1	58–87
41	7/3	55°00′N	155°00′W	28	46.43	53.57	51.0	24–78
42	7/8	58°00′N	145°00′W	53	64.15	35.85	20.6	2–39
43	7/9	58°00′N	145°00′W	17	58.82	41.18	29.8	0–63
44	6/9	50°00′N	135°00′W	28	78.57	21.43	0.0	0–23
45	6/10	50°00′N	135°00′W	31	90.32	9.68	0.0	0–22
46	7/20	51°00′N	135°00′W	85	54.12	45.88	37.8	23–53
47	6/14	54°53′N	134°22′W	15	66.67	33.33	16.3	0–51

[1] Confidence interval truncated at 0 and 100 percent.

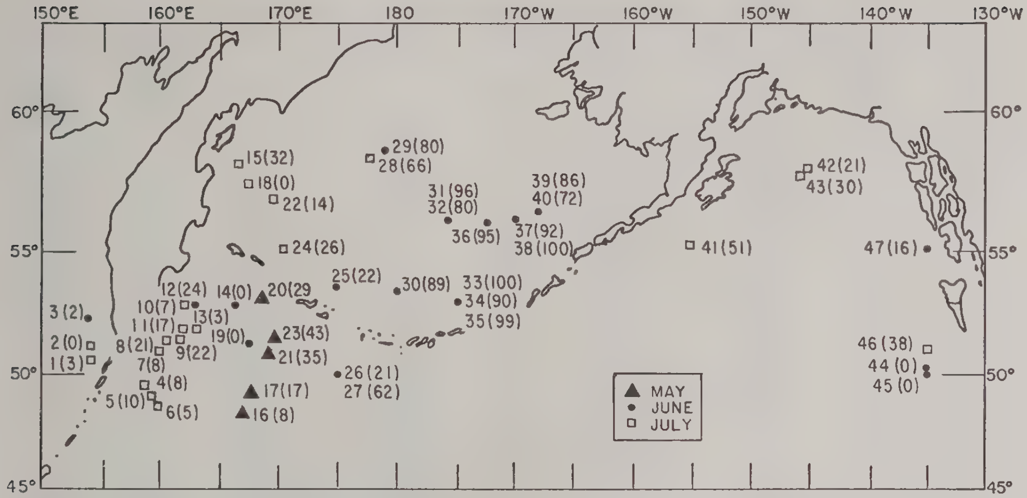

FIGURE 4. Percentages of mature sockeye salmon classified as western Alaskan type in samples collected in May-July 1957. (First number at each locality is sample number; number in parentheses shows percentage western Alaskan type.)

collected over a relatively small area, and the population distributions shown by the 1956 samples have been used to supplement the information obtained in later years.

1957 SAMPLES

In 1957 sampling, coverage was more extensive than in 1956, and more samples containing larger portions of mature salmon were available. The results of classifying the 1957 samples have been given in Table 13, and sample locations have been plotted in Fig. 4.

In May and June western Alaskan type salmon strongly dominated in the Bering Sea west to about longitude 179°00′E. West of this longitude the abundance of western Alaskan fish decreased markedly. Samples taken in the North Pacific Ocean during May as far west as about longitude 165°E, however, indicated the presence of some Alaskan type salmon. Samples 26 and 27 taken two days apart at latitude 50°N, longitude 175°E, had point estimates of 21 and 62 percent western Alaskan type. This difference tentatively could be accounted for both biologically and statistically. Possibly a rapid movement of salmon through the area resulted in sampling of two distinct groups, or the small sample sizes (25 and 20 specimens) could have contributed to a large difference between the point estimates. The large confidence intervals of the samples overlapped to indicate a possibility of similar proportions of western Alaskan type salmon in the two samples.

During July most samples of mature sockeye salmon were collected near the Kamchatka Peninsula. This late in the year the point estimates (Fig. 4) indicated surprisingly high proportions of Alaskan type fish for the area. In this particular area, these could be misclassified fish of Asian stocks not represented in the Asian reference samples.

Of three samples collected in the Gulf of Alaska in June, two contained no western Alaskan type fish, and one (sample 47) was classified as containing 16 percent western Alaskan type salmon. Also the classification results for four samples taken here in July showed large proportions of Kamchatkan fish. These observations could have resulted from sampling variation (most confidence intervals included zero). Supplementary evidence from tagging studies and distance function analysis indicated that this area would be expected to contain mostly sockeye salmon from North American areas other than western Alaska. Such stocks could not be distinguished from Kamchatkan salmon by the applied discriminant function analysis (Fukuhara *et al.*, 1962, p. 42).

1958 SAMPLES

The results of classifying the 1958 samples are listed in Table 14. During May and June (Fig. 5), samples were collected from the Gulf of Alaska to the Okhotsk Sea. No samples were available from approximately longitude 172°W to 173°E. Some intermingling of populations existed in the North Pacific Ocean between longitudes 160°E and 175°E. Samples taken in the Gulf of Alaska indicated the presence of some Kamchatkan fish, but again these probably were misidentified fish from North American areas other than

TABLE 14. Classification of mature sockeye salmon: 1958 high seas samples.

		Position			Percentage classified			
Sample number	Sampling date	Latitude	Longitude	Size of sample	Kamchatkan type	Western Alaskan type	Corrected percent western Alaskan type	90 percent confidence limits[1]
1	7/5	50°49′N	153°07′E	113	72.57	27.43	0.0	0–14
2	6/25	51°09′N	153°40′E	119	67.23	32.77	8.1	0–23
3	6/15	51°08′N	153°45′E	116	81.03	18.97	0.0	0–14
4	7/15	51°39′N	154°10′E	119	63.87	36.13	15.0	0–30
5	7/5	48°55′N	156°28′E	110	61.82	38.18	19.3	4–35
6	7/19	50°35′N	159°50′E	113	63.72	36.28	15.3	0–31
7	7/26	51°58′N	159°51′E	115	66.09	33.91	10.5	0–26
8	6/16	49°21′N	160°27′E	108	63.89	36.11	15.0	0–31
9	6/25	49°35′N	166°35′E	108	64.81	35.19	13.1	0–29
10	6/21	59°02′N	167°00′E	19	84.21	15.79	0.0	0–35
11	6/15	50°41′N	167°14′E	109	71.56	28.44	0.0	0–15
12	5/16	50°10′N	168°15′E	114	55.26	44.74	32.8	17–49
13	6/17	59°16′N	169°03′E	20	90.00	10.00	0.0	0–34
14	5/26	47°30′N	169°41′E	105	62.86	37.14	17.1	1–33
15	7/31	59°18′N	170°38′E	83	84.34	15.66	0.0	0–17
16	5/29	51°05′N	171°30′E	99	72.73	27.27	0.0	0–15
17	6/5	52°02′N	171°35′E	95	53.68	46.32	36.0	19–53
18	6/7	50°50′N	172°30′E	112	41.96	58.04	60.1	44–76
19	5/16	49°21′N	173°19′E	95	53.68	46.32	36.0	19–53
20	6/18	56°00′N	172°30′W	73	31.51	68.49	81.7	63–100
21	6/26	55°58′N	170°04′W	21	19.05	80.95	100.0	69–100
22	6/17	53°30′N	170°02′W	48	29.17	70.83	86.5	64–100
23	6/25	55°04′N	169°24′W	72	29.17	70.83	86.5	68–100
24	6/15	55°00′N	155°00′W	84	36.90	63.10	70.6	53–88
25	6/7	55°00′N	150°00′W	71	38.03	61.97	68.2	49–88
26	6/9	55°00′N	150°00′W	18	38.89	61.11	66.5	28–100
27	6/8	55°00′N	150°00′W	27	48.15	51.85	47.4	15–80
28	6/4	58°00′N	145°00′W	62	70.97	29.03	0.4	0–20
29	6/5	58°00′N	145°00′W	73	63.01	36.99	16.8	0–36

[1] Confidence interval truncated at 0 and 100 percent.

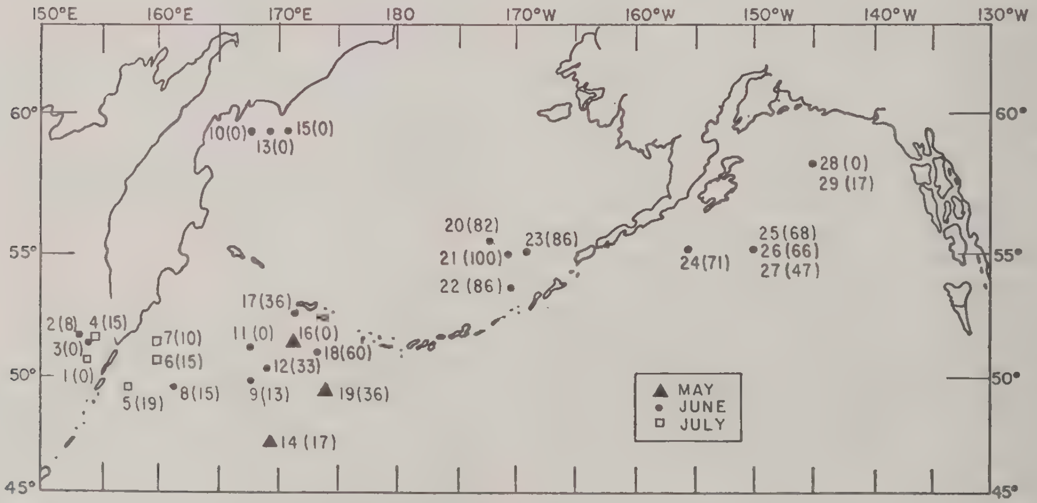

FIGURE 5. Percentages of mature sockeye salmon classified as western Alaskan type in samples collected in May-July 1958. (First number at each locality is sample number; number in parentheses shows percentage western Alaskan type.)

TABLE 15. Classification of mature sockeye salmon : 1959 high seas samples.

		Position			Percentage classified			
Sample number	Sampling date	Latitude	Longitude	Size of sample	Kamchatkan type	Western Alaskan type	Corrected percent western Alaskan type	90 percent confidence limits[1]
1	6/15	49°48′N	159°41′E	19	52.63	47.37	27.0	0–74
2	6/17	49°31′N	159°51′E	15	66.67	33.33	0	0–51
3	6/15	48°31′N	162°31′E	94	58.51	41.49	12.2	0–33
4	7/5	52°32′N	163°48′E	22	72.73	27.27	0	0–42
5	6/15	48°24′N	163°55′E	99	66.67	33.33	0	0–20
6	6/8	48°07′N	165°11′E	33	72.73	27.27	0	0–35
7	6/5	46°21′N	168°06′E	72	70.83	29.17	0	0–24
8	7/15	48°48′N	168°36′E	42	57.14	42.86	15.6	0–47
9	5/27	48°00′N	169°12′E	84	69.05	30.95	0	0–22
10	5/26	48°57′N	169°29′E	101	65.35	34.65	0	0–20
11	5/26	48°00′N	170°00′E	39	61.54	38.46	4.6	0–37
12	8/1	58°00′N	170°00′E	17	35.29	64.71	70.5	23–100
13	6/25	49°06′N	170°52′E	19	57.89	42.11	13.7	0–60
14	6/5	53°30′N	171°00′E	35	40.00	60.00	58.7	24–93
15	6/6	53°20′N	171°00′E	55	56.36	43.64	17.6	0–45
16	6/8	55°00′N	171°00′E	61	47.54	52.46	39.7	13–66
17	6/5	51°21′N	171°20′E	84	46.43	53.57	42.5	20–65
18	5/28	50°25′N	171°20′E	21	71.42	28.58	0.0	0–44
19	5/27	48°20′N	172°08′E	26	50.00	50.00	33.6	0–74
20	7/5	56°49′N	173°22′E	95	41.05	58.95	56.0	35–77
21	7/4	58°00′N	175°00′E	23	78.26	21.74	0.0	0–41
22	7/22	51°30′N	175°00′E	20	25.00	75.00	96.4	56–100
23	5/22	51°00′N	175°00′E	38	44.73	55.27	46.8	13–80
24	5/23	50°00′N	175°00′E	16	50.00	50.00	33.6	0–85
25	5/24	49°00′N	175°00′E	20	60.00	40.00	8.4	0–54
26	5/25	48°00′N	175°00′E	20	45.00	55.00	46.1	1–92
27	5/20	51°30′N	175°03′E	20	55.00	45.00	21.0	0–67
28	6/23	52°59′N	179°55′E	62	22.58	77.42	100.0	78–100
29	6/30	60°00′N	180°	15	46.67	53.33	41.9	0–95
30	6/28	58°00′N	180°	17	47.06	52.94	40.9	0–91
31	6/27	57°00′N	180°	111	39.64	60.36	59.6	40–79
32	6/26	56°00′N	180°	125	28.00	72.00	88.8	72–100
33	6/25	55°00′N	180°	51	33.33	66.67	75.4	48–100
34	6/24	54°00′N	180°	19	21.05	78.95	100.0	60–100
35	6/13	53°30′N	180°	65	26.15	73.85	93.5	71–100
36	6/2	51°00′N	180°	73	27.39	72.61	90.4	69–100
37	6/3	49°59′N	179°57′W	21	28.58	71.42	87.4	47–100
38	6/18	56°00′N	179°00′W	36	36.11	63.89	68.5	35–100
39	6/22	52°38′N	178°47′W	42	42.85	57.15	51.5	20–83
40	7/27	51°31′N	176°42′W	22	59.09	40.91	10.7	0–54
41	7/29	51°29′N	176°38′W	34	82.35	17.65	0.0	0–34
42	6/14	51°32′N	176°34′W	47	29.78	70.22	84.4	57–100
43	6/12	51°32′N	176°31′W	132	31.06	68.94	81.1	64–98
44	6/15	51°31′N	176°25′W	115	37.39	62.61	65.2	47–84
45	6/24	56°00′N	176°00′W	92	28.26	71.74	88.2	69–100
46	6/23	55°00′N	176°00′W	86	19.77	80.23	100.0	81–100
47	6/22	54°00′N	176°00′W	96	27.08	72.92	91.1	72–100
48	6/25	57°00′N	175°00′W	105	33.33	66.67	75.4	56–94
49	6/15	56°00′N	175°00′W	20	15.00	85.00	100.0	61–100
50	6/21	52°59′N	175°00′W	32	50.00	50.00	33.6	0–70
51	5/28	51°41′N	171°57′W	68	29.42	70.58	85.3	62–100

Continued . . .

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[1] Confidence interval truncated at 0 and 100 percent.

TABLE 15. Continued.

Sample number	Sampling date	Position		Size of sample	Percentage classified		Corrected percent western Alaskan type	90 percent confidence limits[1]
		Latitude	Longitude		Kamchatkan type	Western Alaskan type		
52	7/2	53°58′N	170°01′W	18	38.89	61.11	61.5	14–100
53	6/27	59°00′N	170°00′W	56	48.21	51.79	38.1	10–66
54	6/28	58°00′N	170°00′W	54	27.78	72.22	89.4	64–100
55	6/30	55°59′N	170°00′W	117	30.77	69.23	81.9	64–100
56	7/5	51°00′N	169°56′W	32	40.62	59.38	57.1	21–93
57	5/27	51°56′N	169°39′W	52	36.53	63.47	67.4	40–95
58	7/11	53°30′N	165°00′W	31	48.39	51.61	37.6	0–75
59	7/12	52°58′N	164°58′W	28	53.57	46.43	24.6	0–64
60	7/26	53°55′N	159°40′W	29	17.24	82.76	100.0	67–100

western Alaska. Four samples collected in the eastern Bering Sea in June contained an average of 88 percent western Alaskan type salmon. Few samples were collected in July because of the low abundance of mature sockeye on the high seas in the latter part of the season except in some areas near the coast lines. Mature salmon in five samples taken near the southeastern and southwestern coasts of the Kamchatka Peninsula in July were classified as 0 to 19 percent western Alaskan type fish. As suggested earlier salmon classified as western Alaskan type in these particular samples could belong to Asian populations not included in the reference samples.

1959 SAMPLES

The results of classifying the 1959 samples are listed in Table 15. The sample locations and percentages of western Alaskan type salmon have been shown in Figure 6.

May and June sampling was much more extensive than in previous years, particularly in the Bering Sea. Samples of mature sockeye from this area were col-

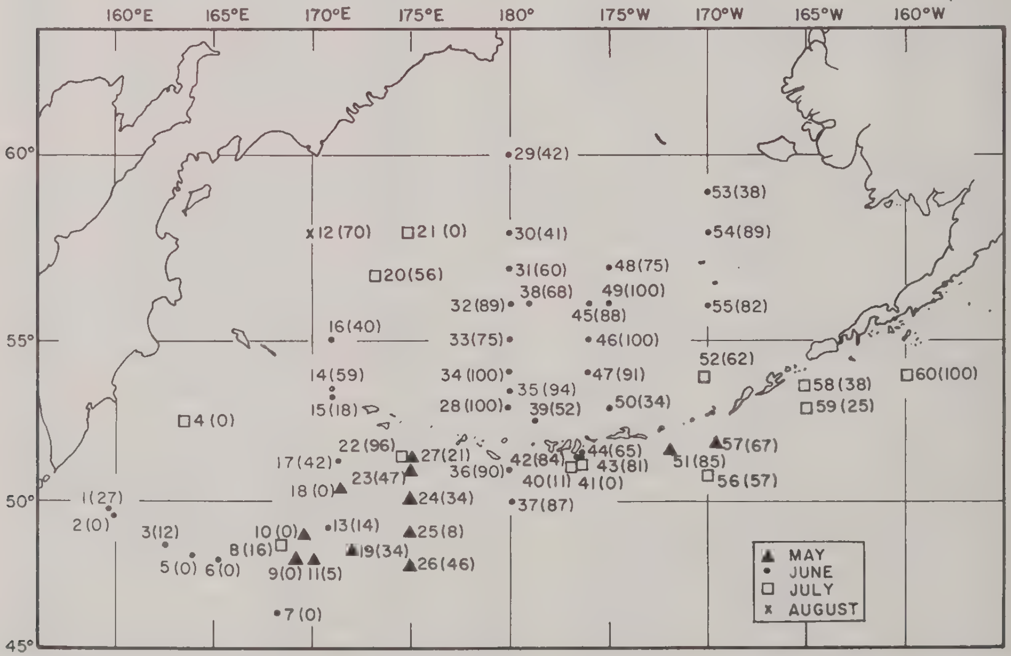
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FIGURE 6. Percentages of mature sockeye salmon classified as western Alaskan type in samples collected in May-August 1959. (First number at each locality is sample number; number in parentheses shows percentage western Alaskan type.)

TABLE 16. Classification of mature sockeye salmon: 1960 high seas samples.

Sample number	Sampling date	Position		Size of sample	Percentage classified		Corrected percent western Alaskan type	90 percent confidence limits[1]
		Latitude	Longitude		Kamchatkan type	Western Alaskan type		
1	7/14	49°58′N	160°50′E	38	57.89	42.11	29.5	4–55
2	7/6	49°22′N	162°43′E	103	64.08	35.92	17.5	2–33
3	6/3	52°37′N	164°18′E	117	77.78	22.22	0.0	0–13
4	6/18	53°13′N	164°44′E	101	77.23	22.77	0.0	0–14
5	7/11	50°46′N	166°48′E	103	68.93	31.07	8.0	0–23
6	5/28	46°32′N	167°47′E	220	62.27	37.73	21.0	10–32
7	6/9	52°40′N	168°00′E	25	44.00	56.00	56.6	25–88
8	6/8	51°00′N	168°00′E	23	73.91	26.09	0.0	0–30
9	6/10	54°06′N	169°43′E	28	46.43	53.57	51.9	22–82
10	5/31	53°02′N	170°00′E	26	42.31	57.69	59.9	29–91
11	5/30	52°00′N	170°00′E	36	55.56	44.44	34.1	8–61
12	5/28	50°07′N	170°04′E	53	50.94	49.06	43.1	21–65
13	5/30	52°42′N	171°37′E	113	59.29	40.71	26.8	12–42
14	6/28	59°41′N	173°42′E	107	69.16	30.84	7.5	0–22
15	6/8	53°37′N	175°54′E	33	21.21	78.79	100.0	77–100
16	6/23	54°57′N	179°23′E	40	32.50	67.50	79.0	55–100
17	6/6	51°00′N	179°59′E	115	30.43	69.57	83.1	69–97
18	6/5	50°02′N	179°59′E	47	42.55	57.45	59.4	36–82
19	6/21	55°00′N	178°52′W	20	30.00	70.00	83.9	51–100
20	6/7	51°04′N	178°30′W	117	17.95	82.05	100.0	88–100
21	6/15	53°17′N	178°17′W	119	15.97	84.03	100.0	88–100
22	6/11	52°24′N	178°00′W	28	71.42	28.58	3.1	0–30
23	6/19	54°03′N	177°05′W	164	17.68	82.32	100.0	90–100
24	6/20	55°01′N	176°58′W	121	14.05	85.95	100.0	88–100
25	6/18	53°00′N	176°58′W	111	11.71	88.29	100.0	87–100
26	7/4	51°20′N	176°45′W	19	57.89	42.11	29.5	0–66
27	8/14	51°28′N	176°30′W	31	16.13	83.87	100.0	76–100
28	8/18	50°40′N	176°30′W	16	18.75	81.25	100.0	67–100
29	6/15	53°00′N	176°10′W	114	17.54	82.46	100.0	88–100
30	6/28	58°28′N	176°07′W	116	25.00	75.00	93.7	81–100
31	6/16	54°01′N	175°38′W	113	15.04	84.96	100.0	88–100
32	6/18	56°01′N	175°00′W	60	28.33	71.67	87.2	68–100
33	6/19	57°01′N	174°59′W	39	15.38	84.62	100.0	79–100
34	6/20	56°42′N	173°27′W	120	24.17	75.83	95.3	83–100
35	7/11	51°29′N	173°04′W	30	40.00	60.00	64.4	36–93
36	7/12	51°09′N	173°01′W	33	30.30	69.70	83.3	58–100
37	7/7	53°44′N	173°00′W	36	30.56	69.44	82.8	58–100
38	7/13	50°50′N	172°59′W	17	23.53	76.47	96.5	64–100
39	6/21	56°21′N	171°41′W	113	22.12	77.88	99.3	87–100
40	5/24	50°06′N	171°40′W	83	25.30	74.70	93.1	78–100
41	5/23	51°04′N	170°49′W	114	21.93	78.07	99.7	87–100
42	6/27	51°18′N	170°37′W	39	33.33	66.67	77.4	53–100
43	7/18	50°54′N	170°02′W	31	41.94	58.06	60.6	32–89
44	6/23	55°00′N	170°01′W	93	23.66	76.34	96.3	82–100
45	7/20	51°32′N	170°10′W	48	33.33	66.67	77.4	56–99
46	7/23	52°15′N	170°00′W	35	40.00	60.00	64.4	38–91
47	6/22	55°58′N	169°59′W	120	15.00	85.00	100.0	88–100
48	6/24	54°00′N	169°59′W	120	34.17	65.83	75.8	62–90
49	6/25	53°20′N	169°59′W	116	21.55	78.45	100.0	88–100
50	7/21	51°51′N	169°59′W	33	63.64	36.36	18.3	0–45
51	6/26	52°15′N	169°57′W	53	39.62	60.38	65.2	44–87
52	7/25	53°05′N	166°05′W	29	62.07	37.93	21.4	0–50

[1] Confidence interval truncated at 0 and 100 percent.

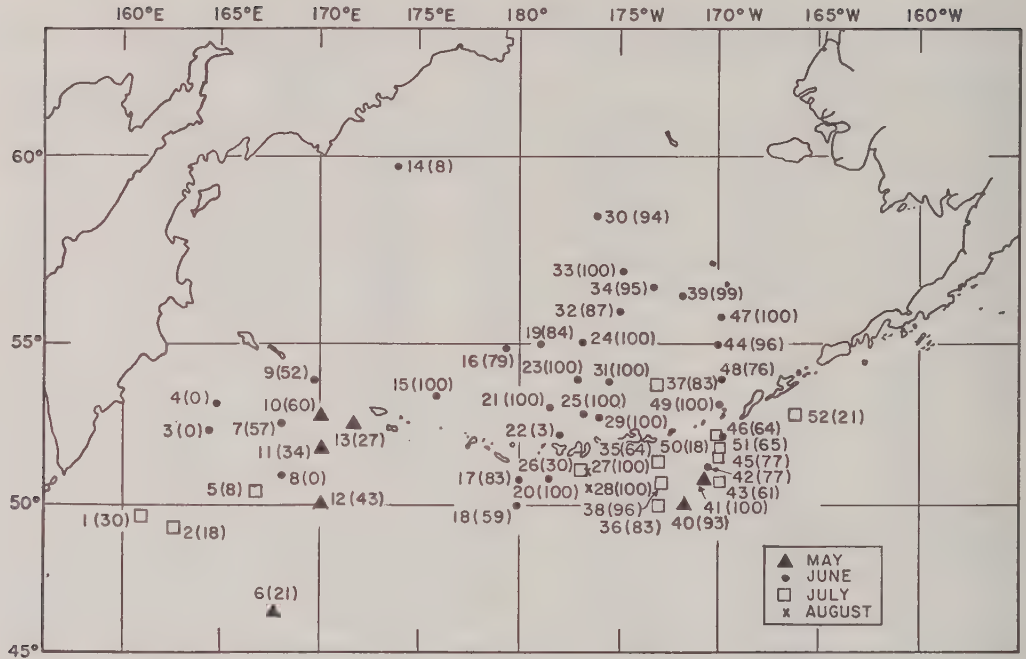
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Figure 7. Percentages of mature sockeye salmon classified as western Alaskan type in samples collected in May-August 1960. (First number at each locality is sample number; number in parentheses shows percentage western Alaskan type.)

lected from longitude 170°W to 171°E and were dominated by western Alaskan type fish at least to longitude 180°. Only five of the 20 samples contained less than 50 percent western Alaskan type fish, and three of the five (samples 29, 30, and 53) were taken at northerly locations where it was possible that stocks not represented in the reference samples would be present. In the North Pacific Ocean, western Alaskan sockeye salmon dominated westward to longitude 180°; samples were classified as 65 to 90 percent western Alaskan type. West of longitude 180°, proportions of western Alaskan type salmon declined to a range of 0 to 59 percent.

Samples were scattered and few in July and August owing to the scarcity of mature fish so late in the season. Only four samples were collected in the Bering Sea. Point estimates for nine samples taken in the North Pacific Ocean varied from 0 to 96 percent western Alaskan type salmon, and the classification of samples did not demonstrate a population-distribution pattern comparable to that found in May and June. Such variability in the classifications is probably attributable to small sample sizes. Other possible explanations for for the inconsistencies in classification of samples from these waters are discussed later.

1960 SAMPLES

The results of analyzing the 1960 collections are given in Table 16. Most samples of mature sockeye salmon were collected in May and June in both the Bering Sea and North Pacific Ocean (Fig. 7). Classification of samples from the Bering Sea showed an overwhelming predominance of western Alaskan type salmon. Sample 22, however, which contained 28 specimens taken at latitude 52°24′N, longitude 178°W, was composed of only 3 percent western Alaskan type sockeye. Possibly most of the salmon in this sample were of Asian origin, but the classification could also be attributable to the presence of salmon from a local population of one of the nearby Aleutian Islands. The single sample (37) collected in the Bering Sea in July was classified as 83 percent western Alaskan type.

In the North Pacific Ocean, samples were available from longitudes 169°18′W to 164°18′E. Rather high percentages of western Alaskan type sockeye salmon appeared in samples taken as far west as longitude 168°E. These samples were collected in late May and early June, and mature western Alaskan salmon possibly could have been this far west. In July and August samples were collected in the North Pacific Ocean between longitudes 169°58′W and 176°45′W;

TABLE 17. Classification of mature sockeye salmon : 1961 high seas samples.

Sample number	Sampling date	Position		Size of sample	Percentage classified		Corrected percent western Alaskan type	90 percent confidence limits[1]
		Latitude	Longitude		Kamchatkan type	Western Alaskan type		
1	7/5	49°21′N	162°11′E	107	62.62	37.38	1.0	0–18
2	6/28	50°17′N	162°48′E	96	63.54	36.46	0	0–18
3	7/5	51°59′N	165°59′E	109	66.97	33.03	0	0–16
4	6/29	48°38′N	166°09′E	74	60.81	39.19	4.9	0–25
5	5/30	52°25′N	170°14′E	102	42.16	57.84	45.4	28–63
6	6/22	51°36′N	171°35′E	89	66.29	33.71	0	0–18
7	6/22	50°48′N	171°55′E	87	65.52	34.48	0	0–18
8	6/7	50°40′N	176°17′E	98	32.35	67.35	66.1	49–83
9	6/25	59°00′N	180°	30	50.00	50.00	28.4	0–61
10	6/22	56°00′N	180°	48	25.00	75.00	82.7	60–100
11	6/16	52°38′N	179°46′W	120	20.00	80.00	93.5	80–100
12	6/14	53°35′N	179°18′W	93	29.03	70.97	73.9	57–91
13	6/19	53°15′N	178°06′W	70	25.71	74.29	81.1	62–100
14	6/18	53°46′N	176°37′W	66	33.33	66.67	64.6	44–85
15	6/7	51°07′N	175°33′W	114	31.58	68.42	68.4	53–84
16	6/13	54°00′N	175°00′W	109	32.11	67.89	67.2	51–83
17	6/22	55°05′N	170°03′W	118	24.58	75.42	83.6	69–98
18	6/19	58°20′N	170°00′W	46	28.26	71.74	75.6	52–99
19	6/16	56°11′N	170°00′W	59	28.81	71.19	74.4	53–96
20	6/14	55°09′N	170°00′W	146	21.23	78.77	90.8	79–100
21	6/23	54°27′N	170°00′W	37	35.14	64.86	60.7	33–89
22	6/24	53°56′N	170°00′W	45	13.33	86.67	100.0	80–100
23	6/12	53°25′N	170°00′W	52	19.23	80.77	95.2	76–100
24	6/17	57°47′N	169°58′W	119	18.49	81.51	96.8	84–100
25	6/25	53°26′N	169°57′W	62	22.58	77.42	87.9	69–100
26	5/16	51°38′N	166°48′W	103	23.30	76.70	86.4	72–100
27	5/15	52°26′N	166°28′W	78	32.05	67.95	67.4	48–86
28	6/30	54°59′N	165°06′W	32	12.50	87.50	100.0	76–100
29	6/29	55°59′N	165°00′W	117	17.95	82.05	98.0	85–100
30	7/9	54°00′N	162°30′W	33	54.54	45.45	18.5	0–49
31	6/8	53°40′N	160°24′W	169	22.49	77.51	88.1	77–100
32	6/15	55°03′N	156°00′W	72	36.11	63.89	58.5	38–79
33	5/5	55°00′N	155°00′W	41	36.59	63.41	57.5	31–84

[1] Confidence interval truncated at 0 and 100 percent.

of these, most were dominated by western Alaskan type salmon. Because of the scarcity of maturing fish at this time of year, many samples were small; the accuracy of the point estimates can be judged by noting the large confidence intervals.

1961 SAMPLES

In 1961, only 33 high seas samples were available for analysis (Table 17). These samples were collected from May 5 to July 9. Eighteen were from the Bering Sea and 15 from the North Pacific Ocean along the length of the Aleutian Islands (Fig. 8).

In the Bering Sea no samples were available from areas west of longitude 180°. The percentages of western Alaskan type salmon in samples from the Bering Sea were high (61 to 100 percent), except for sample 9, taken at latitude 59°00′N, longitude 180°, which classified as only 28 percent Alaskan type. This sample contained only 30 specimens, and the confidence interval for the estimate was 0 to 61 percent. Again, the most probable interpretation of the classification is that the sample contained sockeye salmon from Asian or North American streams not originally included in the reference populations. Similar classifications occurred in this same general northern portion of the sampling area in previous years. West of longitude 170°00′W, only four samples were available; these were classified as predominantly (88 to 100 percent) western Alaskan salmon.

The classification of samples taken over a wide expanse in the North Pacific Ocean was generally similar to that of samples taken in preceding years throughout

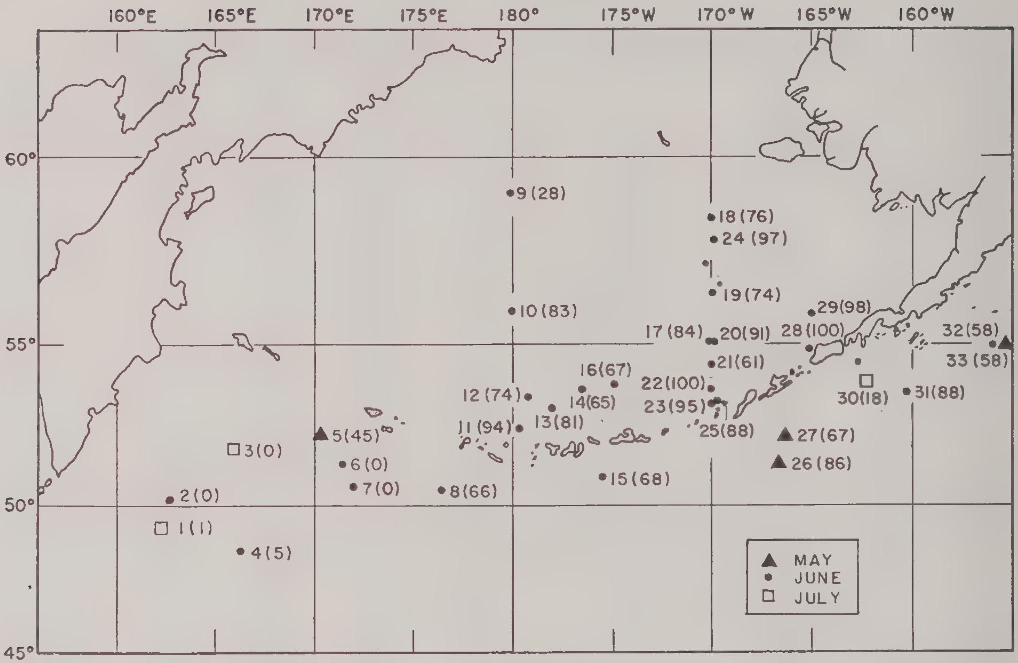

FIGURE 8. Percentages of mature sockeye salmon classified as western Alaskan type in samples collected in May-July 1961. (First number at each locality is sample number; number in parentheses shows percentage western Alaskan type.)

the area. However, sample 30 taken July 9 at latitude 54°00′N, longitude 162°30′W, indicated only a small proportion of western Alaskan type fish (18 percent). Because of the late date and the area of collection of this sample, it seems unlikely that Kamchatkan salmon were actually present. It is more reasonable to hold that the classification was a consequence of departure from the assumption that only sockeye salmon originating in western Alaskan or Kamchatkan streams occurred in the marine waters sampled. This rationale, however, does not eliminate the possibility that Kamchatkan salmon were present in the sample. Samples taken in the Gulf of Alaska had rather low proportions of western Alaskan type fish, and the preceding evaluations may also be applied to these samples.

1962 Samples

Table 18 presents the classificatory data on the 39 samples taken from the North Pacific Ocean and Bering Sea in 1962. Sample locations are shown in Figure 9.

The classifications generally were similar to those of previous years; western Alaskan type salmon predominated from eastern areas westward to approximately longitude 175°E. A large group of samples were available from an area west of longitude 170°E and south of latitude 50°N. With one exception, there was little indication that western Alaskan sockeye salmon were in this area. Sample 11, taken on May 25 at latitude 46°17′N, longitude 169°53′E, was classified as 67 percent western Alaskan type. Possibly western Alaskan salmon were present here during this time of the year, for they conceivably could have reached spawning grounds in western Alaska near the peak of the Bristol Bay runs. Nevertheless, the classification could have been influenced by the presence of fish of an Asian stock which morphologically resembled western Alaskan salmon. Further sampling for a sustained period of time, especially in early spring, in these far western oceanic areas will be necessary to evaluate conclusively the significance of such situations.

Summary of High Seas Distribution

Figure 10 summarizes the sampling and high seas distribution of mature Kamchatkan and western Alaskan type sockeye salmon collected in 1956–62. During these years considerable sampling was accomplished north of latitude 46°N in the North Pacific Ocean and also in the Bering Sea from longitudes 180° to 170°W. The conspicuous lack of samples west of longitude 180° in the Bering Sea is discussed later.

TABLE 18. Classification of mature sockeye salmon: 1962 high seas samples.

Sample number	Sampling date	Position		Size of sample	Percentage classified		Corrected percent western Alaskan type	90 percent confidence limits[1]
		Latitude	Longitude		Kamchatkan type	Western Alaskan type		
1	6/12	49°35′N	166°26′E	113	66.37	33.63	0.0	0–16
2	6/12	49°22′N	166°36′E	113	62.83	37.17	3.9	0–20
3	6/16	53°18′N	166°55′E	213	63.38	36.62	2.7	0–15
4	6/12	48°32′N	167°41′E	103	61.17	38.83	7.6	0–25
5	6/18	48°26′N	167°48′E	87	64.37	35.63	0.5	0–19
6	6/18	48°26′N	167°58′E	95	57.89	42.11	14.8	0–33
7	6/12	48°20′N	168°12′E	110	64.55	35.45	0.1	0–17
8	6/12	47°42′N	168°15′E	88	71.59	28.41	0.0	0–18
9	5/25	47°10′N	168′50′E	92	66.30	33.70	0.0	0–18
10	5/25	47°23′N	169°20′E	96	70.83	29.17	0.0	0–18
11	5/25	46°17′N	169°53′E	196	34.18	65.82	67.0	55–79
12	6/12	47°14′N	169°56′E	58	65.52	34.48	0.0	0–23
13	6/3	51°00′N	170°00′E	70	62.86	37.14	3.8	0–25
14	5/25	52°16′N	170°12′E	107	60.75	39.25	8.5	0–26
15	6/1	52°00′N	170°12′E	43	65.12	34.88	0.0	0–26
16	5/25	52°30′N	170°23′E	104	59.62	40.38	11.0	0–28
17	6/25	51°10′N	170°41′E	33	63.64	36.36	2.1	0–32
18	6/28	50°53′N	171°11′E	35	57.14	42.86	16.4	0–47
19	6/10	50°23′N	171°18′E	194	60.31	39.69	9.5	0–22
20	5/25	49°50′N	171°18′E	104	53.85	46.15	23.7	6–41
21	5/25	50°02′N	171°27′E	108	37.04	62.96	60.7	44–78
22	5/31	50°15′N	173°55′E	115	42.61	57.39	48.4	32–65
23	5/31	50°30′N	174°04′E	118	35.59	64.41	63.9	48–80
24	6/5	51°00′N	176°00′E	37	40.54	59.46	53.0	24–82
25	6/6	49°47′N	176°12′E	82	68.29	31.71	0.0	0–19
26	6/6	51°20′N	176°21′E	110	30.91	69.09	74.2	58–90
27	6/6	49°33′N	176°45′E	74	60.81	39.19	8.3	0–29
28	6/6	51°20′N	176°57′E	111	25.23	74.77	86.7	72–100
29	6/6	50°56′N	177°26′E	109	39.45	60.55	55.4	38–72
30	6/6	50°26′N	177°26′E	116	31.90	68.10	72.0	56–88
31	6/2	50°09′N	179°37′E	200	49.00	51.00	34.4	22–47
32	6/1	50°32′N	178°33′W	106	30.19	69.81	75.8	60–92
33	6/1	50°46′N	178°25′W	110	35.45	64.55	64.2	48–81
34	6/16	54°01′N	177°07′W	65	12.31	87.69	100.0	82–100
35	5/31	51°22′N	176°04′W	108	32.41	67.59	70.9	55–87
36	6/11	50°57′N	176°00′W	39	46.15	53.85	40.6	12–70
37	6/19	53°28′N	175°57′W	33	33.33	66.67	68.9	39–99
38	5/31	51°14′N	175°22′W	103	26.21	73.79	84.5	69–100
39	7/12	52°52′N	167°07′W	42	28.57	71.43	79.3	54–100

[1] Confidence interval truncated at 0 and 100 percent.

The detailed results presented for each year have indicated similarities in the classification of samples within broad geographical regions. Generally, Kamchatkan type salmon were dominant west of longitude 170°E in the North Pacific Ocean and in the few samples available west of longitude 175°E in the Bering Sea. Neither continental stock was consistently predominant from about longitude 170°E to 180° in the North Pacific Ocean samples. East of longitude 180° the dominance of western Alaskan type salmon was marked. Samples taken from the Gulf of Alaska are included in Figure 10; the validity of the applied discriminant function analysis was questionable, however, for samples taken in this area, as discussed previously.

EVALUATION OF UNDERLYING ASSUMPTIONS

The validity of the conclusions derived from the foregoing analyses depends upon rationalization of the underlying assumptions and the compatibility of the results with certain observations and reasonable hypotheses on the distribution of sockeye salmon. It is in-

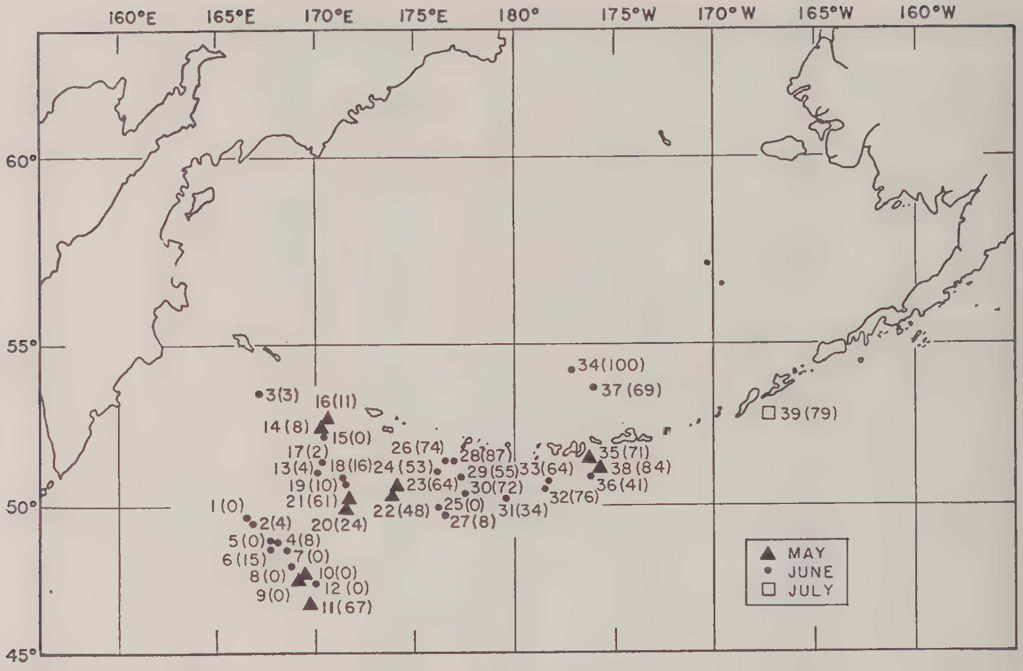
160°E
165°E
170°E
175°E
180°
175°W
170°W
165°W
160°W
60°
55°
50°
45°
1(0)
2(4)
3(3)
4(8)
5(0)
6(15)
7(0)
8(0)
9(0)
10(0)
11(67)
12(0)
13(4)
14(8)
15(0)
16(11)
17(2)
18(16)
19(10)
20(24)
21(61)
22(48)
23(64)
24(53)
25(0)
26(74)
27(8)
28(87)
29(55)
30(72)
31(34)
32(76)
33(64)
34(100)
35(71)
36(41)
37(69)
38(84)
39(79)
▲ MAY
• JUNE
☐ JULY

Figure 9. Percentages of mature sockeye salmon classified as western Alaskan type in samples collected in May-July 1962. (First number at each locality is sample number; number in parentheses shows percentage western Alaskan type.)

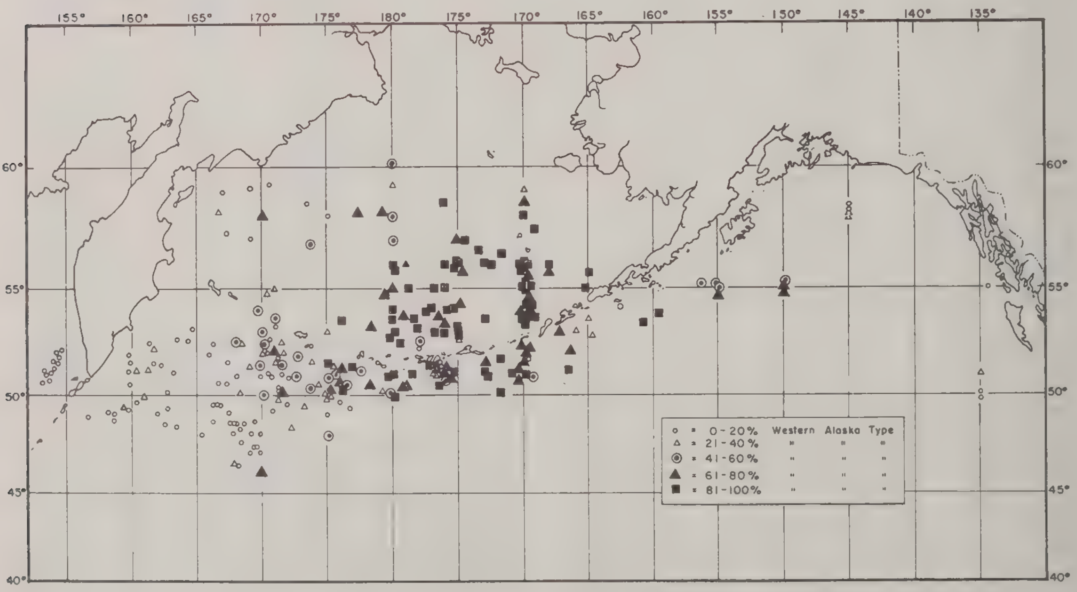
155°
160°
165°
170°
175°
180°
175°
170°
165°
160°
155°
150°
145°
140°
135°
60°
55°
50°
45°
40°
○ = 0-20% Western Alaska Type
△ = 21-40% " " "
◎ = 41-60% " " "
▲ = 61-80% " " "
■ = 81-100% " " "

Figure 10. Summary of the high seas distribution of mature western Alaskan type sockeye salmon, 1956–62 samples.

deed the exceptional biological study in which all assumptions are defined and completely satisfied. The failure to satisfy underlying assumptions completely does not necessarily jeopardize the validity of conclusions. Determining the effect of not satisfying the underlying assumptions, however, is essential. The high seas distribution of mature sockeye salmon stocks of Asia and North America is evaluated in this light.

Sampling of Reference Populations

Ideally, sampling procedures for these studies would have been designed to measure and evaluate fully the components of variance (such as time of sampling and sex and age differences) in meristic characters of stocks from major western Alaskan and Kamchatka Peninsula streams. Since such a study in itself, considering financial and logistical limitations, would be a very ambitious undertaking, we necessarily assumed that the samples obtained adequately represented the meristic characteristics of the western Alaskan and Kamchatkan populations. For reasons discussed in the following paragraphs, the procedure employed has appeared adequate for our purposes.

A rather obvious deficiency in the study was the almost complete lack of stream samples from the principal sockeye salmon rivers of the Kamchatka Peninsula. In lieu of stream collections, samples were obtained from Japanese motherships operating off the southwest and southeast coasts of Kamchatka. Unless intercontinental straying occurred, the time of capture and advanced stages of gonad maturation assured that these sockeye salmon were of Asian origin even though their natal stream was unknown. The differences between the timing of the runs to major east-coast and west-coast streams of the Kamchatka Peninsula (Cleaver, 1964) have indicated that the Okhotsk Sea and the far western North Pacific Ocean were probably dominated at the times sampled by elements of the southwestern Kamchatkan populations.

No samples were available from the streams of east Kamchatka or even from coastal areas near eastern rivers that produce sockeye salmon. Failure to obtain samples which reasonably could be assumed to represent Kamchatka River stocks, however, was not considered to be of great consequence. The run into the Kamchatka River—by far the largest sockeye salmon producer on the east coast of the Kamchatka Peninsula—reportedly occurs rather early (Cleaver, 1964; Taguchi, 1957); the period of active coastal fishing is almost terminated by the end of June. Most samples used in these analyses were taken after the beginning of June and at least 200 miles from the Kamchatka River. If the rate of movement of 12.5 miles per day observed by Sato (1938) for sockeye salmon migrating to Asian streams applied, then the maturing elements of stocks originating in the Kamchatka River would not have been available later than mid-June in any high seas waters, except in those very close to the mouth of the Kamchatka River.

Sampling on the High Seas

Most mature sockeye salmon taken on the high seas during the times of sampling were captured on their spawning migrations. Monitoring the distributions of dynamic populations presented numerous problems; therefore, the point estimates of the respective continental stocks, for samples taken at particular times and places, probably represented extremely transitory phenomena. Since the distribution of mature salmon in time and space would have been systematically related to their later appearance at a particular stream to spawn, the problem of extrapolation from one point of observation to the next was minimal in the easternmost and westernmost waters of the North Pacific Ocean and Bering Sea. The classification in these instances was consistent with the distribution as it would seem to have occurred, if the time required for the respective populations to arrive at their natal streams for spawning is considered.

In areas where intermingling of the continental stocks might occur, the proportions could change rapidly; therefore, studies in these areas require extensive sampling to cope with the complexity of the situation. Evidence of intermingling occurred in the North Pacific Ocean principally between longitudes 170°E and 180°; the paucity of samples from the western Bering Sea prevented detection of intermingling west of longitude 180° and north of the Aleutian Islands. According to Japanese catch statistics in annual reports of the International North Pacific Fisheries Commission for the years 1955–1960 (INPFC, 1956–1961), sockeye salmon were caught in the far western area of the Bering Sea during most years covered by this report, but few samples were received from this area for morphological analyses. As Canadian and U.S. research vessels also were limited in area coverage, the distribution and relative abundance of the two continental stocks in the western Bering Sea remains comparatively unknown.

Intra-Area Variability in Characters

The means of the seven meristic characters from the western Alaskan reference samples collected in 1956 and 1957 were unaffected by internal sources of variation (i.e., sex, time of sampling, freshwater age, ocean age, and year class). When data from samples collected in later years were included, the evident differences in means in some characters indicated lack of homogeneity within the western Alaskan population. Significant year class differences in the later tests were probably attributable, in part, to increased power of the test resulting from the addition of successive data from more year classes, which increased the degrees of freedom. Some heterogeneity among certain components of the river populations may have been undetected in samples from the earlier years. Various components of a river population could be non-randomly sampled which would lead to reference samples not representative of the total population. A discriminant function based on such samples would misclassify western Alaskan fish unless the reference and high seas samples contained the same components proportionately. We assumed that the distribution of within-stream components in offshore samples was proportional to their distribution in the reference samples.

Normality, Common Variance-Covariance

The failure to satisfy completely the assumption of common variance and the absence of a good test for normality in small samples require further evaluation of the effects on the discriminant function analysis of violating these assumptions. Even in the most extreme case of heterogeneity of variance, the largest variance (for lateral line scale counts) was only 3.3 times greater than the smallest. Deviation from normality was not apparent in distributional curves of the meristic characters. Deviations from either assumption probably were not of serious consequence in the discriminant function analysis for the following reasons. First, the observed errors of misclassification in all years for known western Alaskan salmon (i.e., those taken within streams) approximated the theoretical errors of misclassification inherent in the applied discriminant function. Second, it was reasonable to expect that in 1960, before their appearance in Bristol Bay streams, the extremely large runs of sockeye salmon would have been almost totally dominant in the Bering Sea east of longitude 180°. Point estimates of the proportion of western Alaskan type sockeye salmon in samples from this high seas area, with only two exceptions, were greater than 83 percent, and the confidence intervals for the point estimates included 100 percent. Therefore, we concluded that the discriminant function analysis was justified without verification of normality and despite the apparent heterogeneity of characters in some components of the western Alaskan population.

Dominant High Seas Populations

The discriminant function analysis, as applied to the problem of distinguishing sockeye salmon stocks in certain areas of the ocean, classified salmon into two alternative populations: western Alaskan and Kamchatkan salmon. Originally, the assumption of a dichotomous high seas population of sockeye salmon was based on the evidence of tagging and morphological studies conducted before 1958. Subsequent results of these same studies contributed no contrary information, and for most of the area considered, increased the amount of evidence supporting the assumption.

In certain areas, there was some reason to suspect the presence of populations other than the two specified alternatives. Considering the time and location of these collections, one would not reasonably expect mature members of one or the other of the specified populations to be so distant from their spawning areas. In the Gulf of Alaska, salmon classified as Kamchatkan type probably originated in rivers entering the Gulf of Alaska and rivers of southeastern Alaska. Some samples taken off the coasts of Kamchatka during July contained significant numbers of fish that classified as Bristol Bay morphotype which probably points out the inadequacy of our Asian reference samples. All other evidence justified the assumption that most of the mature sockeye salmon in the area of study were from either Bristol Bay or the Kamchatka Peninsula. Other classificatory analyses and racial study techniques would be required to classify accurately any extraneous populations in these areas.

CONCLUSIONS

The following conclusions are drawn regarding the preceding analyses and the high seas distribution of mature sockeye salmon from western Alaska and the Kamchatka Peninsula.

1. Sockeye salmon from principal streams of western Alaska and the Kamchatka Peninsula were widely distributed in the Bering Sea and North Pacific Ocean during the spring and summer in 1956–62. Kamchatkan salmon were numerically dominant in most samples taken west of longitude 175°E in the Bering Sea and North Pacific Ocean. Western Alaskan salmon were predominant in most samples eastward from about longitudes 175°E and 180° in the Bering Sea and North Pacific Ocean. Dominance west of longitude 180° in the Bering Sea was concluded only on the strength of the few available samples. Sockeye salmon from the Kamchatka Peninsula and from western Alaska appeared to intermingle to the greatest extent in samples taken south of the Aleutian Islands between longitudes 170°E and 180°.

2. Limitations of sampling in both time and space precluded more definite delineation of the high seas distribution of mature salmon from Kamchatka and

western Alaska. Further limitations were imposed by failure to satisfy completely the assumption that only western Alaskan and Kamchatkan salmon were present in all samples, particularly those taken from certain areas such as the northern Bering Sea and Gulf of Alaska. It was evident that in these areas an alternative classificatory scheme would be needed to identify sockeye salmon stocks accurately.

3. The use of fish from offshore samples for determination of the morphological characteristics of Kamchatkan salmon probably resulted in inaccuracies in the classificatory procedures. After analysis of tagging data, we considered that the areas sampled in the Okhotsk Sea and off the southeast coast of Kamchatka were dominated by salmon migrating to major sockeye producing streams (primarily the Ozernaya River) on the southwest coast of the Kamchatka Peninsula. We could not, however, determine whether the reference samples accurately reflected the morphological characteristics of the majority of Kamchatkan salmon. Since a large portion of the Kamchatkan sockeye salmon production is taken by the high seas commercial fisheries, inshore samples of mature fish might not truly represent the population characteristics. Because of the high seas fishery, perhaps sampling of these stocks could best be conducted at sea, after we have gained further knowledge of the rates and routes of migration and the relative abundance of major Kamchatkan stocks.

4. Under the limitations imposed by the inherent errors of misclassification in the classificatory procedures, estimates of the variance of the point estimates indicated that the optimum size of samples was 100 to 150 specimens.

5. Empirical evidence suggests that any observed departures from the underlying assumptions of homogeneity of character means within populations and of common variance and normality of meristic characters had little effect on the efficiency of discriminant function analysis in distinguishing the two continental populations.

SUMMARY

To determine the distribution of western Alaskan and Kamchatkan sockeye salmon in the North Pacific Ocean and Bering Sea, meristic characters of sockeye collected from 1955–1962 were examined. Seven characters were treated in a discriminant function analysis: number of scales on the lateral line; total number of vertebrae; position of the first haemal arch; number of ventral gill rakers; total number of gill rakers; number of pectoral fin rays; and number of anal fin rays. This function was developed to discriminate between the principal sockeye salmon stocks of western Alaska and those of Kamchatka Peninsula. The results of the analyses are summarized.

The means of most of the selected characters in the initial development of the discriminant function appeared unaffected by intra-area sources of variation such as the sex or age of the fish. In analyses of data collected later, differences occurred among one or more of these components. Year class differences occurred in five of the seven characters. Such heterogeneity among the components of the western Alaskan population required the assumption that the components of river stocks were distributed throughout the high seas in proportion to their occurrence in the inshore reference samples.

Negligible correlation of meristic characters with fish length indicated that little bias was introduced by the selectivity of gear employed to collect samples.

Two statistical assumptions underlying the discriminant function analysis were examined. No radical departures from normality were observed in the frequency distributions of counts from the meristic characters. Slight discrepancies occurred between the variances of characters obtained from reference samples of western Alaskan and Kamchatkan salmon. Such departures from the assumptions of normality and common variance were considered to affect the efficiency of the discriminant function only slightly at most. The noted departures from assumptions were tested empirically by using the discriminant function to classify samples of sockeye salmon taken in western Alaskan streams in 1957–62. The percentages of correct classification in the stream samples approximated the theoretically expected percentage of correct classification.

On the basis of information from tagging studies and catch statistics, we assumed that streams of the Kamchatka Peninsula and those of western Alaska—principally the tributaries of Bristol Bay—produced the majority of the sockeye salmon in the ocean areas that were investigated most intensively. For mature salmon this assumption has been substantiated, except in particular ocean areas, by additional data from other studies as well as by the analyses of meristic data. Relatively little has been learned, however, about the distribution of immature sockeye salmon; their distribution in time and space is not governed by participation in a spawning migration, as is that of mature fish. Although some high seas samples included immature specimens, only mature sockeye salmon were used in the present study.

The classifications of high seas samples of mature salmon collected in 1956–62 indicate that the distributions of Kamchatkan and western Alaskan sockeye have been consistent from year to year in broad areas of the ocean. Thus, mature Kamchatkan salmon are numerically dominant in the Bering Sea and North Pacific Ocean from the Kamchatka Peninsula eastward to approximately longitude 175°E. East of longitude 175°E to 180°, western Alaskan salmon predominate. Intermingling of the two continental stocks appears greatest between longitudes 170°E and 180° in the North Pacific Ocean.

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APPENDIX

TABLES OF TESTS FOR INTRA-AREA SOURCES OF VARIATION FOR THE SEVEN MERISTIC CHARACTERS AND FIGURES OF FREQUENCY DISTRIBUTIONS FOR THE CHARACTERS FROM ASIAN AND NORTH AMERICAN REFERENCE SAMPLES

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Appendix Table 1a. Effect of sexual dimorphism on number of scales along the lateral line in sockeye salmon collected in 1958.

Area	Date	Age group	Sex	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/1	5_2	M	131.233	30	3.841	0.358	1.421	0.148	1,71	0.690
			F	131.070	43	2.733	0.252				
”	7/31	6_3	M	130.889	27	2.565	0.382	1.013	0.145	1,52	0.700
			F	131.074	27	3.842	0.377				
Kodiak Island											
Karluk R.	6/26	5_3	M	130.538	26	4.340	0.408	1.426	3.302	1,53	0.070
			F	129.655	29	2.379	0.286				
Red R.	6/24	5_3	M	131.294	17	1.344	0.281	1.018	0.806	1,39	0.375
			F	131.667	24	1.970	0.286				
Bristol Bay											
Egegik R.	7/7	5_3	M	130.050	40	3.331	0.288	1.129	0.376	1,97	0.540
			F	130.288	59	3.760	0.252				
”	7/7	6_3	M	130.111	27	3.027	0.335	1.134	0.006	1,52	0.940
			F	130.148	27	2.670	0.314				
Ugashik R.	7/16	5_2	M	130.708	24	4.217	0.419	1.233	0.527	1,48	0.473
			F	130.308	26	3.420	0.363				
”	7/16	5_3	M	130.875	32	2.952	0.304	1.116	0.455	1,71	0.500
			F	130.610	41	2.645	0.254				
Kvichak R.	7/10	5_3	M	131.625	16	4.247	0.515	1.427	0.018	1,35	0.890
			F	131.524	21	6.060	0.537				
”	7/10	6_3	M	131.839	31	5.607	0.425	1.510	1.556	1,66	0.215
			F	131.189	37	3.714	0.317				
”	7/16	5_3	M	132.353	17	5.994	0.594	1.039	0.160	1,39	0.675
			F	132.667	24	6.230	0.509				
Kvichak R. (Merca Creek)	7/24	5_3	M	131.674	46	7.380	0.400	1.143	0.351	1,99	0.550
			F	131.364	55	6.457	0.343				
Kvichak R. (Merca Creek)	7/24	6_3	M	131.267	30	5.997	0.447	1.738	4.560[a]	1,49	0.040
			F	132.619	21	3.450	0.405				
Wood R.	7/5	4_2	M	130.488	41	3.405	0.288	1.036	0.113	1,120	0.735
			F	130.370	81	3.286	0.201				

$C = -2 \sum \ln P_i = 25.318$

[a] Significant at 5-percent level.

Appendix Table 1b. Effect of sexual dimorphism on number of vertebrae in sockeye salmon collected in 1958.

								F-values			
Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	7/1	5_2	M	67.276	29	0.993	0.185	2.117[a]	0.049	1,70	0.820
			F	67.233	43	0.469	0.144				
”	7/31	6_3	M	67.074	27	0.842	0.176	1.037	3.289	1,52	0.075
			F	67.519	27	0.873	0.180				
Kodiak Island											
Karluk R.	6/26	5_3	M	67.120	25	0.608	0.156	1.330	2.723	1,52	0.108
			F	66.793	29	0.457	0.125				
Red R.	6/24	5_3	M	67.438	16	0.260	0.127	1.908	1.570	1,37	0.215
			F	67.696	23	0.496	0.147				
Bristol Bay											
Egegik R.	7/7	5_3	M	67.050	40	0.459	0.107	1.346	1.629	1,95	0.200
			F	67.246	57	0.618	0.104				
”	7/7	6_3	M	67.115	26	0.588	0.150	1.007	0.024	1,51	0.865
			F	67.148	27	0.592	0.148				
Ugashik R.	7/16	5_2	M	67.000	22	0.762	0.186	1.627	0.018	1,46	0.885
			F	67.038	26	1.240	0.217				
”	7/16	5_3	M	67.452	31	0.590	0.138	1.190	0.003	1,70	0.970
			F	67.439	41	0.702	0.131				
Kvichak R.	7/10	5_3	M	68.063	16	0.993	0.249	1.068	0.562	1,35	0.460
			F	67.810	21	1.060	0.224				
”	7/10	6_3	M	67.742	31	0.730	0.153	1.481	0.398	1,66	0.530
			F	67.595	37	1.081	0.171				
”	7/16	5_3	M	68.167	18	1.324	0.271	1.095	0.057	1,40	0.800
			F	68.083	24	1.209	0.224				
Kvichak R. (Merca Creek)	7/24	5_3	M	67.814	43	1.202	0.167	1.155	0.312	1,93	0.575
			F	67.692	52	1.041	0.141				
Kvichak R. (Merca Creek)	7/24	6_3	M	67.800	30	0.855	0.169	1.4492	2.560	1,48	0.115
			F	68.200	20	0.590	0.172				
Wood R.	7/5	4_2	M	67.175	40	0.713	0.133	1.215	0.537	1,118	0.465
			F	67.288	80	0.587	0.085				

$$C = -2 \sum \ln P_i = 27.150$$

[a] Significant at 5-percent level.

APPENDIX TABLE 1c. Effect of sexual dimorphism on position of the first haemal arch in sockeye salmon collected in 1958.

Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	*F*-values		d. f.	*P*
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/1	5_2	M	34.655	29	0.736	0.159	1.252	0.745	1,70	0.397
			F	34.488	43	0.588	0.117				
”	7/31	6_3	M	34.593	27	0.788	0.171	1.227	0.232	1,52	0.630
			F	34.481	27	0.642	0.154				
Kodiak Island											
Karluk R.	6/26	5_3	M	34.462	26	0.900	0.186	1.565	1.574	1,53	0.214
			F	34.172	29	0.575	0.141				
Red R.	6/24	5_3	M	34.529	17	0.388	0.151	1.624	0.912	1,39	0.350
			F	34.750	24	0.630	0.162				
Bristol Bay											
Egegik R.	7/7	5_3	M	34.550	40	0.715	0.134	1.096	0.717	1,95	0.405
			F	34.702	57	0.784	0.117				
”	7/7	6_3	M	34.333	27	0.615	0.150	1.044	0.264	1,52	0.605
			F	34.444	27	0.642	0.154				
Ugashik R.	7/16	5_2	M	34.375	24	0.504	0.145	1.033	0.002	1,48	0.980
			F	34.385	26	0.488	0.137				
”	7/16	5_3	M	34.806	31	0.360	0.108	2.097[a]	3.336	1,72	0.070
			F	34.488	41	0.755	0.136				
Kvichak R.	7/10	5_3	M	35.000	16	0.933	0.241	2.073	2.009	1,35	0.163
			F	34.619	21	0.450	0.146				
”	7/10	6_3	M	35.000	31	0.533	0.131	1.840	1.587	1,66	0.210
			F	34.730	37	0.981	0.163				
”	7/16	5_3	M	34.500	18	0.853	0.217	1.850	6.398[a]	1,40	0.018
			F	35.125	24	0.461	0.139				
Kvichak R. (Merca Creek)	7/24	5_3	M	35.044	45	0.998	0.149	1.057	0.158	1,97	0.685
			F	34.963	54	1.055	0.140				
Kvichak R. (Merca Creek)	7/24	6_3	M	34.833	30	0.697	0.152	1.034	5.608[a]	1,48	0.023
			F	35.400	20	0.674	0.184				
Wood R.	7/5	4_2	M	34.150	40	0.541	0.116	1.381	0.393	1,118	0.530
			F	34.250	80	0.747	0.096				

$C = -2 \sum \ln P_i = 40.482$

[a] Significant at 5-percent level.

Appendix Table 1d. Effect of sexual dimorphism on number of ventral gill rakers in sockeye salmon collected in 1958.

Area	Date	Age group	Sex	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	7/1	5_2	M	23.233	30	0.669	0.149	1.058	0.464	1,70	0.495
			F	23.048	42	0.632	0.122				
"	7/31	6_3	M	23.037	27	0.577	0.146	1.113	0.762	1,52	0.393
			F	23.222	27	0.642	0.154				
Kodiak Island											
Karluk R.	6/26	5_3	M	22.615	26	0.728	0.167	1.629	0.396	1,53	0.530
			F	22.448	29	1.186	0.202				
Red R.	6/24	5_3	M	22.706	17	0.719	0.206	1.504	0.000	1,39	0.999
			F	22.708	24	0.478	0.141				
Bristol Bay											
Egegik R.	7/7	5_3	M	22.925	40	0.790	0.140	1.287	0.083	1,97	0.770
			F	23.017	59	1.017	0.131				
"	7/7	6_3	M	22.444	27	1.258	0.216	1.480	1.759	1,52	0.187
			F	22.815	27	0.850	0.177				
Ugashik R.	7/16	5_2	M	23.292	24	1.087	0.212	1.847	0.470	1,48	0.495
			F	23.115	26	0.588	0.150				
"	7/16	5_3	M	23.250	32	0.581	0.134	1.804	1.902	1,71	0.170
			F	22.951	41	1.048	0.160				
Kvichak R.	7/10	5_3	M	23.063	16	0.860	0.232	1.755	0.346	1,35	0.555
			F	22.905	21	0.490	0.153				
"	7/10	6_3	M	23.233	30	0.876	0.171	1.179	1.102	1,65	0.295
			F	23.486	37	1.033	0.167				
"	7/16	5_3	M	22.944	18	0.524	0.171	2.141	2.639	1,40	0.113
			F	23.417	24	1.122	0.216				
Kvichak R. (Merca Creek)	7/24	5_3	M	22.867	45	1.118	0.157	1.255	0.001	1,98	0.990
			F	22.873	55	0.891	0.127				
Kvichak R. (Merca Creek)	7/24	6_3	M	23.167	30	0.697	0.152	1.370	5.456[a]	1,49	0.024
			F	22.571	21	0.955	0.213				
Wood R.	7/5	4_2	M	23.098	41	0.840	0.143	1.268	1.060	1,120	0.305
			F	22.901	81	1.065	0.114				

$$C = -2 \sum \ln P_i = 31.207$$

[a] Significant at 5-percent level.

Appendix Table 1e. Effect of sexual dimorphism on total number of gill rakers in sockeye salmon collected in 1958.

								F-values			
Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	7/1	5_2	M	37.600	30	1.559	0.228	1.288	0.762	1,70	0.390
			F	37.357	42	1.210	0.170				
"	7/31	6_3	M	37.185	27	1.235	0.214	0.214	1.060	1,52	0.535
			F	37.370	27	1.165	0.208				
Kodiak Island											
Karluk R.	6/26	5_3	M	36.615	26	1.608	0.249	1.361	1.002	1,53	0.320
			F	36.241	29	2.189	0.275				
Red R.	6/24	5_3	M	37.059	17	2.431	0.120	2.151	0.427	1,39	0.515
			F	36.792	24	1.130	0.217				
Bristol Bay											
Egegik R.	7/7	5_3	M	36.950	40	1.280	0.179	1.525	2.145	1,97	0.165
			F	37.339	59	1.952	0.182				
"	7/7	6_3	M	36.815	27	1.850	0.262	1.179	1.113	1,52	0.295
			F	37.222	27	2.181	0.284				
Ugashik R.	7/16	5_2	M	37.708	24	1.783	0.272	1.372	0.497	1,48	0.483
			F	37.462	26	1.300	0.224				
"	7/16	5_3	M	37.563	32	0.964	0.173	2.458[a]	2.450	1,71	0.120
			F	37.073	41	2.370	0.240				
Kvichak R.	7/10	5_3	M	37.250	16	2.867	0.423	3.629[b]	0.129	1,35	0.715
			F	37.095	21	0.790	0.194				
"	7/10	6_3	M	37.567	30	1.841	0.248	1.159	0.298	1,65	0.573
			F	37.757	37	2.133	0.240				
"	7/16	5_3	M	37.167	18	1.676	0.305	1.518	1.609	1,40	0.210
			F	37.750	24	2.544	0.326				
Kvichak R. (Merca Creek)	7/24	5_3	M	36.911	45	2.536	0.237	1.386	0.014	1,98	0.890
			F	36.945	55	1.830	0.182				
Kvichak R. (Merca Creek)	7/24	6_3	M	37.400	30	1.490	0.223	1.433	3.917	1,49	0.055
			F	36.667	21	2.135	0.319				
Wood R.	7/5	4_2	M	37.341	41	1.980	0.220	1.065	1.122	1,120	0.293
			F	37.062	81	1.859	0.151				

$C = -2 \sum \ln P_i = 31.923$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

APPENDIX TABLE 1f. Effect of sexual dimorphism on number of pectoral fin rays in sockeye salmon in 1958.

								F-values			
Area	Date	Age group	Sex	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	7/1	5_2	M	16.138	29	0.264	0.095	1.217	0.376	1,70	0.540
			F	16.209	43	0.217	0.071				
"	7/31	6_3	M	16.481	27	0.258	0.098	1.000	0.698	1,52	0.410
			F	16.444	27	0.258	0.098				
Kodiak Island											
Karluk R.	6/26	5_3	M	16.520	25	0.258	0.101	1.337	8.711[b]	1,52	0.005
			F	16.138	29	0.193	0.082				
Red R.	6/24	5_3	M	16.529	17	0.388	0.151	1.540	0.097	1,39	0.915
			F	16.583	24	0.252	0.102				
Bristol Bay											
Egegik R.	7/7	5_3	M	16.525	40	0.308	0.088	1.045	0.085	1,97	0.765
			F	16.492	59	0.322	0.074				
"	7/7	6_3	M	16.593	27	0.250	0.096	1.010	0.286	1,52	0.593
			F	16.519	27	0.258	0.097				
Ugashik R.	7/16	5_2	M	16.348	23	0.236	0.101	1.139	0.571	1,47	0.455
			F	16.231	26	0.344	0.115				
"	7/16	5_3	M	16.563	32	0.319	0.099	1.303	2.546	1,71	0.115
			F	16.366	41	0.238	0.076				
Kvichak R.	7/10	5_3	M	16.438	16	0.260	0.127	1.165	0.114	1,35	0.733
			F	16.381	21	0.250	0.109				
"	7/10	6_3	M	16.613	31	0.380	0.110	1.329	8.094[b]	1,66	0.006
			F	16.216	37	0.286	0.088				
"	7/16	5_3	M	16.588	17	0.381	0.150	1.656	1.356	1,39	0.250
			F	16.333	24	0.230	0.097				
Kvichak R. (Merca Creek)	7/24	5_3	M	16.283	46	0.429	0.096	1.292	0.156	1,99	0.690
			F	16.236	55	0.332	0.077				
Kvichak R. (Merca Creek)	7/24	6_3	M	16.367	30	0.310	0.101	1.216	0.163	1,49	0.680
			F	16.429	21	0.255	0.110				
Wood R.	7/5	4_2	M	16.512	41	0.305	0.086	1.191	5.194[a]	1,120	0.022
			F	16.284	81	0.256	0.056				

$C = -2 \sum \ln P_i = 44.044$[a]

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 1g. Effect of sexual dimorphism on number of anal fin rays in sockeye salmon collected in 1958.

Area	Date	Age group	Sex	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/1	5_2	M	18.067	30	0.410	0.117	1.737	0.578	1,71	0.455
			F	18.163	43	0.236	0.074				
»	7/31	6_3	M	18.444	27	0.335	0.111	1.206	0.049	1,52	0.820
			F	18.407	27	0.404	0.122				
Kodiak Island											
Karluk R.	6/26	5_3	M	18.077	26	0.312	0.109	1.003	0.032	1,53	0.855
			F	18.103	29	0.311	0.135				
Red R.	6/24	5_3	M	18.471	17	0.387	0.151	1.586	0.119	1,38	0.730
			F	18.391	23	0.614	0.163				
Bristol Bay											
Egegik R.	7/7	5_3	M	18.237	38	0.457	0.110	1.079	1.143	1,97	0.293
			F	18.085	59	0.493	0.091				
»	7/7	6_3	M	18.222	27	0.412	0.124	1.359	0.025	1,51	0.865
			F	18.192	26	0.560	0.147				
Ugashik R.	7/16	5_2	M	18.000	24	0.435	0.134	1.088	0.029	1,48	0.855
			F	17.808	26	0.400	0.124				
»	7/16	5_3	M	17.875	32	0.306	0.097	1.020	9.145[b]	1,71	0.004
			F	18.268	41	0.300	0.085				
Kvichak R.	7/10	5_3	M	18.563	16	0.393	0.156	1.145	5.524[b]	1,35	0.025
			F	18.048	21	0.450	0.146				
»	7/10	6_3	M	18.167	30	0.421	0.118	1.059	0.115	1,64	0.733
			F	18.111	36	0.446	0.111				
»	7/16	5_3	M	18.611	18	0.488	0.165	1.868	4.688[a]	1,40	0.040
			F	18.208	24	0.261	0.104				
Kvichak R. (Merca Creek)	7/24	5_3	M	18.196	46	0.560	0.110	1.038	0.004	1,98	0.970
			F	18.204	54	0.581	0.103				
Kvichak R. (Merca Creek)	7/24	6_3	M	18.200	30	0.234	0.088	1.944	1.219	1,49	0.275
			F	18.429	21	0.455	0.147				
Wood R.	7/5	4_2	M	18.150	40	0.490	0.110	1.531	0.037	1,119	0.840
			F	18.173	81	0.320	0.062				

$C = -2 \sum \ln P_i = 34.444$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

APPENDIX TABLE 1h. Effect of sexual dimorphism on number of scales along the lateral line in sockeye salmon collected in 1959.

Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	*F*-values		d. f.	*P*
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	6/29	6_3	M	130.824	34	6.754	0.446	1.566	0.092	1,80	0.760
			F	130.667	48	4.313	0.300				
"	8/2	6_3	M	131.385	13	1.592	0.349	1.576	0.119	1,36	0.735
			F	131.560	25	2.508	0.316				
Kodiak Island											
Red R.	6/25	6_3	M	131.735	49	3.533	0.268	1.354	0.274	1,71	0.600
			F	131.500	24	2.609	0.330				
Bristol Bay											
Naknek R.	7/2	5_3	M	130.119	109	3.587	0.182	1.690	0.252	1,140	0.614
			F	129.939	33	2.122	0.253				
Egegik R.	7/7	5_3	M	130.444	45	2.025	0.212	1.686	0.715	1,94	0.405
			F	130.157	51	3.414	0.259				
"	7/7	6_3	M	130.118	17	2.612	0.392	1.021	0.000	1,41	0.995
			F	130.115	26	2.668	0.321				
Ugashik R.	7/11	5_3	M	130.591	44	2.805	0.253	1.050	0.116	1,81	0.733
			F	130.718	39	2.945	0.276				
"	7/11	6_3	M	130.724	29	1.493	0.226	1.884	0.000	1,74	0.995
			F	130.723	47	2.813	0.245				
Kvichak R.	7/9	4_2	M	130.400	15	4.829	0.567	1.199	1.666	1,31	0.205
			F	131.444	18	5.788	0.567				
"	7/9	5_3	M	130.988	85	3.464	0.202	1.270	0.338	1,188	0.559
			F	130.819	105	4.400	0.205				
"	7/14	5_3	M	129.963	27	2.577	0.308	1.566	10.763[a]	1,72	0.002
			F	131.447	47	4.035	0.293				
"	7/26	5_3	M	130.952	42	2.437	0.241	1.211	0.004	1,82	0.965
			F	130.976	42	2.951	0.264				
Wood R.	6/29	4_2	M	129.927	55	5.032	0.302	1.603	0.588	1,118	0.447
			F	129.646	65	3.139	0.182				

$C = -2 \sum \ln P_i = 52.518$

[a] Significant at 1-percent level.

Appendix Table 1i. Effect of sexual dimorphism on number of vertebrae in sockeye salmon collected in 1959.

								F-values			
Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	6/29	6_3	M	67.324	34	1.073	0.179	1.250	0.461	1,78	0.500
			F	67.174	46	0.858	0.138				
"	8/2	6_3	M	67.462	13	0.267	0.141	3.781	0.109	1,36	0.738
			F	67.560	25	1.008	0.200				
Kodiak Island											
Red R.	6/25	6_3	M	67.522	46	0.922	0.141	2.562	0.040	1,65	0.886
			F	67.476	21	0.360	0.130				
Bristol Bay											
Naknek R.	7/2	5_3	M	67.113	106	0.672	0.077	1.655	0.284	1,137	0.588
			F	67.030	33	0.406	0.110				
Egegik R.	7/7	5_3	M	67.140	43	0.600	0.118	1.330	0.030	1,94	0.854
			F	67.170	53	0.798	0.122				
"	7/7	6_3	M	67.176	17	0.406	0.155	1.674	0.831	1,41	0.373
			F	66.962	26	0.680	0.161				
Ugashik R.	7/11	5_3	M	67.024	42	0.561	0.114	1.367	0.258	1,79	0.613
			F	67.103	39	0.410	0.100				
"	7/11	6_3	M	67.345	29	0.307	0.100	1.559	0.584	1,75	0.452
			F	67.229	48	0.479	0.100				
Kvichak R.	7/9	4_2	M	67.067	15	1.064	0.266	1.232	2.020	1,31	0.165
			F	67.611	18	1.312	0.270				
"	7/9	5_3	M	67.476	84	0.590	0.084	1.398	0.337	1,186	0.556
			F	67.404	104	0.825	0.089				
"	7/14	5_3	M	66.880	25	0.608	0.155	1.630	8.591[a]	1,70	0.004
			F	67.553	47	0.991	0.145				
"	7/26	5_3	M	67.488	42	0.705	0.130	1.280	0.060	1,80	0.804
			F	67.439	41	0.902	0.148				
Wood R.	6/29	4_2	M	67.161	56	1.084	0.138	1.168	0.091	1,120	0.758
			F	67.106	66	0.928	0.118				

$C = -2 \sum \ln P_i = 44.442$

[a] Significant at 1-percent level.

Appendix Table 1j. Effect of sexual dimorphism on position of first haemal arch in sockeye salmon collected in 1959.

								F-values			
Area	Date	Age group	Sex	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	6/29	6_3	M	34.706	34	0.821	0.155	1.266	2.326	1,78	0.133
			F	34.413	46	0.649	0.118				
”	8/2	6_3	M	34.692	13	0.400	0.176	1.479	0.730	1,36	0.404
			F	34.480	25	0.592	0.155				
Kodiak Island											
Red R.	6/25	6_3	M	34.438	48	0.932	0.138	1.244	0.033	1,69	0.895
			F	34.391	23	1.159	0.224				
Bristol Bay											
Naknek R.	7/2	5_3	M	34.551	107	0.703	0.077	1.363	2.970	1,38	0.093
			F	34.273	33	0.516	0.126				
Egegik R.	7/7	5_3	M	34.535	43	0.636	0.122	1.603	0.027	1,94	0.851
			F	34.566	53	1.019	0.138				
”	7/7	6_3	M	34.412	17	0.506	0.173	1.117	0.021	1,42	0.876
			F	34.444	27	0.565	0.145				
Ugashik R.	7/11	5_3	M	34.591	44	0.758	0.130	2.462[b]	0.406	1,81	0.525
			F	34.487	39	0.308	0.089				
”	7/11	6_3	M	34.759	29	0.761	0.161	1.117	1.439	1,75	0.235
			F	34.521	48	0.681	0.118				
Kvichak R.	7/9	4_2	M	34.200	15	0.886	0.243	1.771	1.092	1,31	0.324
			F	34.500	18	0.500	0.167				
”	7/9	5_3	M	34.741	85	0.432	0.071	1.728[a]	0.358	1,187	0.547
			F	34.673	104	0.747	0.084				
”	7/14	5_3	M	34.346	26	0.716	0.167	1.172	2.068	1,71	0.161
			F	34.660	47	0.839	0.134				
”	7/26	5_3	M	34.738	42	0.929	0.148	1.247	0.206	1,81	0.647
			F	34.829	41	0.745	0.134				
Wood R.	6/29	4_2	M	34.339	56	0.593	0.100	1.136	0.072	1,120	0.885
			F	34.303	66	0.522	0.089				

$C = -2 \sum \ln P_i = 41.056$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 1k. Effect of sexual dimorphism on number of ventral gill rakers in sockeye salmon collected in 1959.

Area	Date	Age group	Sex	Mean	N	Variance	Standard error	*F*-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	6/29	6_3	M	23.235	34	0.912	0.170	1.237	0.010	1,79	0.920
			F	23.213	47	1.128	0.155				
”	8/2	6_3	M	23.154	13	1.308	0.318	1.180	0.054	1,36	0.814
			F	23.240	25	1.108	0.210				
Kodiak Island											
Red R.	6/25	6_3	M	22.600	50	1.102	0.148	1.465	0.073	1,72	0.783
			F	22.667	24	0.752	0.176				
Bristol Bay											
Naknek R.	7/2	5_3	M	22.945	109	0.868	0.089	1.509	0.350	1,140	0.551
			F	23.061	33	1.309	0.200				
Egegik R.	7/7	5_3	M	22.800	45	1.073	0.155	1.706	0.002	1,96	0.980
			F	22.792	53	0.629	0.110				
”	7/7	6_3	M	23.412	17	0.756	0.210	1.429	0.560	1,42	0.460
			F	23.185	27	1.081	0.200				
Ugashik R.	7/11	5_3	M	23.068	44	0.670	0.122	1.293	0.717	1,81	0.406
			F	23.231	39	0.866	0.148				
”	7/11	6_3	M	23.000	29	1.286	0.210	1.425	0.262	1,76	0.606
			F	22.878	49	0.902	0.134				
Kvichak R.	7/9	4_2	M	23.000	15	0.857	0.239	1.297	0.025	1,31	0.870
			F	22.944	18	1.112	0.248				
”	7/9	5_3	M	23.012	85	0.750	0.095	1.192	0.025	1,188	0.865
			F	22.990	105	0.894	0.089				
”	7/14	5_3	M	22.963	27	0.731	0.164	1.013	0.148	1,73	0.703
			F	23.042	48	0.721	0.122				
”	7/26	5_3	M	22.476	42	0.939	0.148	1.816	0.324	1,82	0.568
			F	22.619	42	1.705	0.200				
Wood R.	6/29	4_2	M	23.000	56	0.946	0.130	1.022	0.114	1,121	0.733
			F	22.940	67	0.967	0.118				

$C = -2 \sum \ln P_i = 36.298$

Appendix Table 11. Effect of sexual dimorphism on total number of gill rakers in sockeye salmon collected in 1959.

Area	Date	Age group	Sex	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	6/29	6_3	M	37.676	34	2.103	0.248	1.049	0.574	1,79	0.455
			F	37.426	47	2.206	0.217				
"	8/2	6_3	M	37.231	13	2.358	0.425	1.118	1.093	1,36	0.298
			F	37.760	25	2.108	0.290				
Kodiak Island											
Red R.	6/25	6_3	M	36.740	50	2.359	0.217	1.455	0.041	1,72	0.833
			F	36.667	24	1.622	0.261				
Bristol Bay											
Naknek R.	7/2	5_3	M	36.890	109	1.766	0.126	1.170	1.717	1,140	0.280
			F	37.242	33	2.066	0.248				
Egegik R.	7/7	5_3	M	37.333	45	2.273	0.224	1.582	0.211	1,96	0.644
			F	37.208	53	1.436	0.164				
"	7/7	6_3	M	38.118	17	1.112	0.255	1.891	2.741	1,42	0.108
			F	37.444	27	2.104	0.279				
Ugashik R.	7/11	5_3	M	37.545	44	1.509	0.184	1.355	0.888	1,81	0.354
			F	37.821	39	2.045	0.228				
"	7/11	6_3	M	37.207	29	3.386	0.342	1.609	0.246	1,76	0.618
			F	37.020	49	2.104	0.207				
Kvichak R.	7/9	4_2	M	37.133	15	1.121	0.274	2.145	0.160	1,31	0.681
			F	36.944	18	2.406	0.366				
"	7/9	5_3	M	37.388	85	1.740	0.141	1.120	0.001	1,188	0.994
			F	37.381	105	1.950	0.134				
"	7/14	5_3	M	37.111	27	1.873	0.263	1.338	1.174	1,73	0.282
			F	37.438	48	1.400	0.170				
"	7/26	5_3	M	36.310	42	1.878	0.212	1.991	0.004	1,82	0.965
			F	36.333	42	3.739	0.298				
Wood R.	6/29	4_2	M	37.214	56	1.662	0.173	1.348	0.019	1,121	0.883
			F	37.179	67	2.241	0.182				

$C = -2 \sum \ln P_i = 41.664$

Appendix Table 1m. Effect of sexual dimorphism on number of pectoral fin rays in sockeye salmon collected in 1959.

								F-values			
Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	6/29	6_3	M	16.294	34	0.336	0.100	1.075	1.006	1,80	0.322
			F	16.167	48	0.313	0.077				
”	8/2	6_3	M	16.308	13	0.567	0.210	1.658	0.361	1,36	0.550
			F	16.440	25	0.342	0.118				
Kodiak Island											
Red R.	6/25	6_3	M	16.580	50	0.290	0.077	1.111	0.085	1,72	0.770
			F	16.542	24	0.261	0.105				
Bristol Bay											
Naknek R.	7/2	5_3	M	16.231	108	0.310	0.055	1.218	2.368	1,138	0.127
			F	16.063	32	0.255	0.089				
Egegik R.	7/7	5_3	M	16.578	45	0.386	0.089	1.322	0.339	1,96	0.560
			F	16.509	53	0.292	0.077				
”	7/7	6_3	M	16.625	16	0.380	0.155	1.136	0.138	1,41	0.709
			F	16.556	27	0.335	0.110				
Ugashik R.	7/11	5_3	M	16.409	44	0.340	0.089	1.008	0.152	1,81	0.694
			F	16.359	39	0.342	0.095				
”	7/11	6_3	M	16.414	29	0.393	0.118	1.154	0.373	1,75	0.540
			F	16.500	48	0.340	0.084				
Kvichak R.	7/9	4_2	M	16.333	15	0.379	0.158	1.149	0.072	1,31	0.786
			F	16.278	18	0.329	0.134				
”	7/9	5_3	M	16.471	85	0.371	0.063	1.063	1.386	1,189	0.243
			F	16.368	106	0.350	0.055				
”	7/14	5_3	M	16.222	27	0.412	0.122	1.124	1.055	1,73	0.321
			F	16.375	48	0.366	0.089				
”	7/26	5_3	M	16.190	42	0.402	0.100	1.813	0.152	1,82	0.694
			F	16.143	42	0.220	0.071				
Wood R.	6/29	4_2	M	16.255	55	0.378	0.084	1.416	0.080	1,120	0.775
			F	16.284	67	0.267	0.063				

$C = -2 \sum \ln P_i = 45.222$

APPENDIX TABLE 1n. Effect of sexual dimorphism on number of anal fin rays in sockeye salmon collected in 1959.

								F-values			
Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	6/29	6_3	M	18.088	34	0.203	0.077	1.970	1.317	1,79	0.256
			F	18.234	47	0.400	0.089				
"	8/2	6_3	M	18.154	13	0.142	0.105	1.706	0.223	1,36	0.635
			F	18.080	25	0.242	0.100				
Kodiak Island											
Red R.	6/25	6_3	M	18.520	50	0.418	0.089	1.203	0.156	1,72	0.684
			F	18.458	24	0.348	0.118				
Bristol Bay											
Naknek R.	7/2	5_3	M	18.093	108	0.440	0.063	1.483	0.887	1,139	0.353
			F	18.212	33	0.297	0.095				
Egegik R.	7/7	5_3	M	17.932	44	0.577	0.114	1.522	1.059	1,95	0.319
			F	18.075	53	0.379	0.084				
"	7/7	6_3	M	18.176	17	0.281	0.126	1.504	1.294	1,42	0.262
			F	17.963	27	0.423	0.126				
Ugashik R.	7/11	5_3	M	18.023	44	0.349	0.089	1.473	0.001	1,81	0.994
			F	18.026	39	0.237	0.077				
"	7/11	6_3	M	18.241	29	0.261	0.095	1.438	0.531	1,76	0.470
			F	18.143	49	0.375	0.089				
Kvichak R.	7/9	4_2	M	18.333	15	0.521	0.187	2.333	4.509[a]	1,31	0.043
			F	17.889	18	0.224	0.110				
"	7/9	5_3	M	17.953	85	0.426	0.071	1.151	1.536	1,188	0.215
			F	18.067	105	0.370	0.063				
"	7/14	5_3	M	18.074	27	0.535	0.141	1.133	0.004	1,72	0.965
			F	18.085	47	0.472	0.100				
"	7/26	5_3	M	17.905	42	0.478	0.105	1.166	3.929	1,81	0.051
			F	18.195	41	0.410	0.100				
Wood R.	6/29	4_2	M	18.375	56	0.420	0.089	1.092	3.914[a]	1,120	0.049
			F	18.136	66	0.454	0.084				

$C = -2 \sum \ln P_i = 57.002$

[a] Significant at 5-percent level.

Appendix Table 1o. Effect of sexual dimorphism on number of scales along the lateral line in sockeye salmon collected in 1960.

								F-values			
Area	Date	Age group	Sex	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/2	4_2	M	131.288	59	3.898	0.275	1.167	0.013	1,98	0.900
			F	131.244	41	3.340	0.285				
”	7/8	4_2	M	130.628	43	3.762	0.295	1.205	6.505[a]	1,104	0.022
			F	131.556	63	3.123	0.224				
”	7/21	4_2	M	130.762	21	5.390	0.507	1.485	5.746[a]	1,85	0.020
			F	131.970	66	3.629	0.234				
Wood R.	7/7	4_2	M	130.424	33	3.191	0.312	1.189	0.024	1,73	0.865
			F	130.357	42	3.795	0.300				
Egegik R.	7/11	4_2	M	130.364	44	3.167	0.268	1.569	0.018	1,96	0.890
			F	130.407	54	2.019	0.192				
”	7/11	5_3	M	130.353	17	2.494	0.384	1.068	0.075	1,42	0.780
			F	130.222	27	2.335	0.293				
Naknek R.	7/7	4_2	M	130.600	75	3.595	0.219	1.027	0.840	1,98	0.367
			F	130.200	25	3.500	0.374				
”	7/7	5_3	M	130.120	25	12.775	0.715	2.305	0.251	1,38	0.625
			F	129.600	15	5.543	0.608				
Ugashik R.	7/14	4_2	M	130.239	92	3.304	0.190	1.088	1.566	1,165	0.214
			F	130.600	75	3.595	0.219				
Branch R.	7/8	4_2	M	129.852	54	2.921	0.232	1.003	1.679	1,156	0.195
			F	129.481	104	2.913	0.167				

$$C = -2 \sum \ln P_i = 25.986$$

[a] Significant at 5-percent level.

Appendix Table 1p. Effect of sexual dimorphism on number of vertebrae in sockeye salmon collected in 1960.

								F-values			
Area	Date	Age group	Sex	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/2	4_2	M	67.500	58	0.921	0.126	1.522	0.299	1,96	0.580
			F	67.400	40	0.605	0.122				
”	7/8	4_2	M	67.220	41	0.675	0.126	1.075	2.577	1,104	0.112
			F	67.477	65	0.628	0.100				
”	7/21	4_2	M	67.217	23	0.359	0.126	1.803	6.209[a]	1,83	0.017
			F	67.677	62	0.648	0.100				
Wood R.	7/7	4_2	M	67.152	33	0.569	0.130	1.302	0.093	1,74	0.760
			F	67.209	43	0.740	0.130				
Egegik R.	7/11	4_2	M	67.171	41	0.395	0.100	1.330	0.014	1,91	0.900
			F	67.154	52	0.526	0.100				
”	7/11	5_3	M	66.941	17	0.681	0.200	1.205	1.351	1,42	0.252
			F	67.222	27	0.565	0.145				
Naknek R.	7/7	4_2	M	67.338	74	0.720	0.100	1.055	2.363	1,98	0.130
			F	67.038	26	0.760	0.170				
”	7/7	5_3	M	67.160	25	1.892	0.276	3.516[a]	0.050	1,37	0.820
			F	67.071	14	0.531	0.195				
Ugashik R.	7/14	4_2	M	67.125	96	0.595	0.077	1.142	0.449	1,168	0.503
			F	67.203	74	0.520	0.084				
Branch R.	7/8	4_2	M	67.107	56	0.680	0.110	1.097	0.428	1,155	0.512
			F	67.020	101	0.620	0.077				

$C = -2 \sum \ln P_i = 24.324$

[a] Significant at 5-percent level.

APPENDIX TABLE 1q. Effect of sexual dimorphism on position of the first haemal arch in sockeye salmon collected in 1960.

								F-values			
Area	Date	Age group	Sex	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d.f.	*P*
Bristol Bay											
Kvichak R.	7/2	4_2	M	34.707	58	0.702	0.110	1.160	1.375	1,97	0.244
			F	34.512	41	0.605	0.122				
”	7/8	4_2	M	34.595	42	0.490	0.110	1.485	0.176	1,105	0.673
			F	34.662	65	0.728	0.105				
”	7/21	4_2	M	34.696	23	1.404	0.247	3.066[b]	0.506	1,84	0.475
			F	34.841	63	0.458	0.084				
Wood R.	7/7	4_2	M	34.382	34	0.848	0.158	1.471	0.067	1,76	0.790
			F	34.432	44	0.577	0.114				
Egegik R.	7/11	4_2	M	34.333	42	0.471	0.105	1.483	0.187	1,93	0.660
			F	34.264	53	0.698	0.114				
”	7/11	5_3	M	34.588	17	0.756	0.210	1.177	0.016	1,42	0.898
			F	34.556	27	0.642	0.155				
Naknek R.	7/7	4_2	M	34.784	74	0.747	0.100	1.130	6.598[a]	1,98	0.013
			F	34.269	26	0.844	0.179				
”	7/7	5_3	M	34.440	25	1.508	0.245	5.866[b]	0.229	1,38	0.629
			F	34.600	15	0.257	0.130				
Ugashik R.	7/14	4_2	M	34.344	96	0.650	0.084	1.252	1.211	1,170	0.274
			F	34.474	76	0.519	0.084				
Branch R.	7/8	4_2	M	34.339	56	0.520	0.095	1.028	0.973	1,157	0.328
			F	34.456	103	0.506	0.071				

$C = -2 \sum \ln P_i = 21.051$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 1r. Effect of sexual dimorphism on number of ventral gill rakers in sockeye salmon collected in 1960.

								F-values			
Area	Date	Age group	Sex	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/2	4_2	M	23.067	60	1.012	0.130	1.002	0.073	1,99	0.782
			F	23.122	41	1.010	0.158				
"	7/8	4_2	M	23.023	44	0.860	0.141	1.151	0.135	1,107	0.712
			F	23.092	65	0.991	0.122				
"	7/21	4_2	M	23.261	23	0.927	0.200	1.109	0.018	1,86	0.890
			F	23.231	65	0.836	0.114				
Wood R.	7/7	4_2	M	22.636	33	1.675	0.226	1.416	0.230	1,74	0.628
			F	22.767	43	1.183	0.167				
Egegik R.	7/11	4_2	M	22.727	44	0.714	0.126	1.165	0.637	1,96	0.431
			F	22.870	54	0.832	0.122				
"	7/11	5_3	M	22.706	17	1.094	0.253	1.554	0.071	1,42	0.785
			F	22.630	27	0.704	0.161				
Naknek R.	7/7	4_2	M	22.784	74	0.637	0.095	1.413	2.199	1,98	0.141
			F	22.500	26	0.900	0.187				
"	7/7	5_3	M	22.920	25	0.908	0.190	1.272	0.072	1,38	0.784
			F	23.000	15	0.714	0.219				
Ugashik R.	7/14	4_2	M	23.135	96	0.960	0.100	1.180	1.046	1,170	0.308
			F	22.987	76	0.813	0.105				
Branch R.	7/8	4_2	M	22.536	56	0.834	0.122	1.124	0.021	1,157	0.880
			F	22.515	103	0.742	0.084				

$C = -2 \sum \ln P_i = 11.518$

Appendix Table 1s. Effect of sexual dimorphism on total number of gill rakers in sockeye salmon collected in 1960.

								F-values			
Area	Date	Age group	Sex	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/2	4_2	M	37.467	60	2.592	0.207	1.470	0.327	1,99	0.565
			F	37.293	41	1.763	0.207				
"	7/8	4_2	M	37.045	44	2.044	0.214	1.142	1.191	1,107	0.275
			F	37.338	65	1.791	0.167				
"	7/21	4_2	M	37.739	23	2.291	0.316	1.109	0.617	1,86	0.438
			F	37.462	65	2.066	0.179				
Wood R.	7/7	4_2	M	36.576	33	3.003	0.302	1.194	0.752	1,74	0.394
			F	36.907	43	2.514	0.241				
Egegik R.	7/11	4_2	M	36.659	44	1.300	0.173	1.615	0.196	1,96	0.655
			F	36.778	54	2.100	0.197				
"	7/11	5_3	M	36.588	17	1.381	0.285	1.251	0.042	1,42	0.883
			F	36.519	27	1.104	0.202				
Naknek R.	7/7	4_2	M	36.315	73	1.331	0.134	1.262	1.340	1,97	0.252
			F	36.000	26	1.680	0.255				
"	7/7	5_3	M	36.560	25	2.008	0.283	1.528	0.308	1,38	0.576
			F	36.800	15	1.314	0.297				
Ugashik R.	7/14	4_2	M	37.177	96	1.810	0.138	1.181	0.675	1,170	0.418
			F	37.013	76	1.533	0.141				
Branch R.	7/8	4_2	M	36.071	56	1.486	0.161	1.041	0.755	1,157	0.392
			F	35.895	103	1.547	0.122				

$C = -2 \sum \ln P_i = 15.810$

Appendix Table 1t. Effect of sexual dimorphism on number of pectoral fin rays in sockeye salmon collected in 1960.

Area	Date	Age group	Sex	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Bristol Bay											
Kvichak R.	7/2	4_2	M	16.500	60	0.322	0.071	1.335	1.674	1,99	0.198
			F	16.341	41	0.430	0.100				
"	7/8	4_2	M	16.409	44	0.433	0.100	1.377	0.100	1,107	0.750
			F	16.446	65	0.314	0.071				
"	7/21	4_2	M	16.435	23	0.441	0.138	1.191	0.002	1,89	0.990
			F	16.441	68	0.370	0.071				
Wood R.	7/7	4_2	M	16.412	34	0.309	0.095	1.016	0.537	1,76	0.466
			F	16.318	44	0.314	0.084				
Egegik R.	7/11	4_2	M	16.364	44	0.284	0.077	1.084	0.011	1,96	0.925
			F	16.352	54	0.308	0.077				
"	7/11	5_3	M	16.706	17	0.219	0.114	1.133	4.492[a]	1,41	0.040
			F	16.385	26	0.248	0.100				
Naknek R.	7/7	4_2	M	16.200	75	0.324	0.063	1.172	0.661	1,99	0.422
			F	16.308	26	0.380	0.122				
"	7/7	5_3	M	16.120	25	0.275	0.105	1.377	1.354	1,38	0.250
			F	16.333	15	0.379	0.158				
Ugashik R.	7/14	4_2	M	16.427	96	0.310	0.055	1.030	1.575	1,169	0.212
			F	16.320	75	0.301	0.063				
Branch R.	7/8	4_2	M	16.125	56	0.256	0.063	1.200	0.569	1,158	0.455
			F	16.058	104	0.308	0.055				

$C = -2 \sum \ln P_i = 16.525$

[a] Significant at 5-percent level.

Appendix Table 1u. Effect of sexual dimorphism on number of anal fin rays in sockeye salmon collected in 1960.

								F-values			
Area	Date	Age group	Sex	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/2	4_2	M	18.333	60	0.463	0.089	1.351	0.597	1,99	0.445
			F	18.220	41	0.625	0.122				
”	7/8	4_2	M	18.318	44	0.500	0.105	1.368	0.042	1,107	0.880
			F	18.292	65	0.366	0.077				
”	7/21	4_2	M	18.217	23	0.723	0.176	1.893[a]	0.097	1,88	0.755
			F	18.269	67	0.382	0.077				
Wood R.	7/7	4_2	M	18.121	33	0.484	0.122	1.498	0.069	1,75	0.787
			F	18.159	44	0.323	0.084				
Egegik R.	7/11	4_2	M	18.341	44	0.416	0.095	1.226	0.004	1,96	0.975
			F	18.333	54	0.340	0.077				
”	7/11	5_3	M	18.176	17	0.281	0.126	1.736	2.978	1,42	0.090
			F	18.519	27	0.488	0.134				
Naknek R.	7/7	4_2	M	18.227	75	0.393	0.071	1.038	1.213	1,99	0.273
			F	18.385	26	0.408	0.126				
”	7/7	5_3	M	18.000	25	0.583	0.152	1.060	4.663[a]	1,38	0.046
			F	18.533	15	0.550	0.192				
Ugashik R.	7/14	4_2	M	18.323	96	0.516	0.071	1.535	0.211	1,170	0.645
			F	18.276	76	0.336	0.063				
Branch R.	7/8	4_2	M	18.200	55	0.682	0.110	2.134[b]	1.306	1,157	0.257
			F	18.327	104	0.319	0.055				

$C = -2 \sum \ln P_i = 20.132$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

APPENDIX TABLE 2a. Effect of time of sampling on number of scales along the lateral line in sockeye salmon collected in 1958–60.

							F-values			
Year and area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
	1958									
Alaska Peninsula										
Chignik R.	7/1	5_2	131.137	73	3.147	0.208	1.489	1.204	1,86	0.295
	7/31	5_2	130.600	15	2.114	0.376				
"	7/1	6_3	130.710	31	1.347	0.208	2.340[a]	0.583	1,83	0.450
	7/31	6_3	130.981	54	3.151	0.242				
Kodiak Island										
Karluk R.	6/26	5_3	130.073	55	3.441	0.250	1.334	0.832	1,73	0.370
	8/31	5_3	130.500	20	2.579	0.359				
"	6/26	6_4	130.070	43	4.924	0.338	1.267	0.945	1,69	0.335
	8/31	6_4	130.571	28	3.885	0.373				
Bristol Bay										
Naknek R.	7/9	5_3	130.436	39	4.095	0.324	1.222[c]	0.086	2,66	0.918
	7/13	5_3	130.188	16	7.760	0.696				
	7/19	5_3	130.214	14	6.954	0.705				
Kvichak R.	7/10	5_3	131.568	37	5.142	0.378	1.093[c]	2.593	2,176	0.117
	7/16	5_3	132.537	41	6.005	0.383				
	7/24	5_3	131.505	101	6.843	0.258				
"	7/10	6_3	131.485	68	4.612	0.260	0.378[c]	2.455	2,155	0.097
	7/16	6_3	132.462	39	4.518	0.340				
	7/24	6_3	131.824	51	5.310	0.323				
			$C = -2 \sum \ln P_i = 17.483$							
	1959									
Alaska Peninsula										
Chignik R.	6/29	6_3	130.732	82	5.260	0.253	2.448[b]	3.577	1,118	0.058
	8/2	6_3	131.500	38	2.149	0.237				
Bristol Bay										
Kvichak R.	7/9	5_3	130.895	190	3.968	0.145	4.632[c]	0.039	2,345	0.963
	7/14	5_3	130.905	74	3.977	0.232				
	7/26	5_3	130.964	74	2.661	0.179				
			$C = -2 \sum \ln P_i = 5.770$							
	1960									
Bristol Bay										
Kvichak R.	7/2	4_2	131.270	100	3.627	0.190	0.938[c]	1.724	2,290	0.208
	7/8	4_2	131.179	106	3.558	0.184				
	7/21	4_2	131.678	87	4.267	0.221				

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

[c] Bartlett's test.

Appendix Table 2b. Effect of time of sampling on number of vertebrae in sockeye salmon collected in 1958–60.

							F-values			
Year and area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
	1958									
Alaska Peninsula										
Chignik R.	7/1	5_2	67.250	72	0.669	0.096	1.164	0.083	1,85	0.770
	7/31	5_2	67.067	15	0.779	0.228				
”	7/1	6_3	67.323	31	0.427	0.117	2.092[a]	0.018	1,83	0.875
	7/31	6_3	67.296	54	0.892	0.128				
Kodiak Island										
Karluk R.	6/26	5_3	66.944	54	0.547	0.100	1.259	4.348[a]	1,71	0.043
	8/31	5_3	67.368	19	0.689	0.190				
”	6/26	6_4	67.023	43	0.643	0.122	1.196	2.170	1,68	0.145
	8/31	6_4	67.333	37	0.769	0.169				
Bristol Bay										
Naknek R.	7/9	5_3	67.333	39	1.124	0.170	0.403[b]	0.010	2,66	0.990
	7/13	5_3	67.313	16	1.427	0.299				
	7/19	5_3	67.286	14	1.454	0.334				
Kvichak R.	7/10	5_3	67.919	37	1.022	0.322	1.088[b]	1.879	2,271	0.080
	7/16	5_3	68.119	42	1.229	0.171				
	7/24	5_3	67.747	95	1.106	0.108				
”	7/10	6_3	67.662	68	0.195	0.367	0.376[b]	3.192[a]	2,151	0.045
	7/16	6_3	68.111	36	0.846	0.153				
	7/24	6_3	67.960	50	0.776	0.124				
			$C = -2 \sum \ln P_i = 22.219$							
	1959									
Alaska Peninsula										
Chignik R.	6/29	6_3	67.238	80	0.943	0.110	1.270	2.445	1,116	0.122
	8/2	6_3	67.526	38	0.743	0.141				
Bristol Bay										
Kvichak R.	7/9	5_3	67.436	188	0.718	0.063	2.130[b]	0.593	2,339	0.640
	7/14	5_3	67.319	72	0.953	0.114				
	7/26	5_3	67.463	82	0.795	0.100				
			$C = -2 \sum \ln P_i = 5.100$							
	1960									
Bristol Bay										
Kvichak R.	7/2	4_2	67.459	98	0.787	0.089	1.676[b]	1.059	2,286	0.358
	7/8	4_2	67.377	106	0.656	0.077				
	7/21	4_2	67.553	85	0.607	0.084				

[a] Significant at 5-percent level.

[b] Bartlett's test.

Appendix Table 2c. Effect of time of sampling on position of the first haemal arch in sockeye salmon collected in 1958–60.

							F-values			
Year and area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
	1958									
Alaska Peninsula										
Chignik R.	7/1	5_2	34.556	72	0.645	0.095	1.284	0.036	1,85	0.845
	7/31	5_2	34.600	15	0.829	0.235				
"	7/1	6_3	34.742	31	0.730	0.153	1.034	1.159	1,83	0.287
	7/31	6_3	34.537	54	0.706	0.114				
Kodiak Island										
Karluk R.	6/26	5_3	34.309	55	0.737	0.116	1.236	0.064	1,72	0.795
	8/31	5_3	34.368	19	0.911	0.219				
"	6/26	6_4	34.674	43	0.795	0.136	1.130	0.429	1,69	0.515
	8/31	6_4	34.536	28	0.704	0.158				
Bristol Bay										
Naknek R.	7/9	5_3	34.625	40	1.010	0.159	0.434[a]	2.544	2,67	0.090
	7/13	5_3	34.375	16	0.780	0.221				
	7/19	5_3	35.000	14	1.077	0.277				
Kvichak R.	7/10	5_3	34.784	37	0.675	0.135	1.383[a]	0.874	2,175	0.446
	7/16	5_3	34.857	42	0.710	0.130				
	7/24	5_3	35.000	99	0.020	0.101				
"	7/10	6_3	34.853	68	0.784	0.107	1.274[a]	1.413	2,152	0.270
	7/16	6_3	35.108	37	0.544	0.121				
	7/24	6_3	35.060	50	0.751	0.122				
			$C = -2 \sum \ln P_i = 13.669$							
	1959									
Alaska Peninsula										
Chignik R.	6/29	6_3	34.538	80	0.733	0.095	1.398	0.009	1,116	0.924
	8/2	6_3	34.553	38	0.524	0.118				
Bristol Bay										
Kvichak R.	7/9	5_3	34.704	189	0.603	0.055	2.852[a]	1.591	2,342	0.232
	7/14	5_3	34.548	73	0.807	0.105				
	7/26	5_3	34.783	83	0.830	0.100				
			$C = -2 \sum \ln P_i = 3.080$							
	1960									
Bristol Bay										
Kvichak R.	7/2	4_2	34.626	99	0.665	0.084	0.564[a]	1.345	2,289	0.277
	7/8	4_2	34.636	107	0.630	0.077				
	7/21	4_2	34.802	86	0.702	0.089				

[a] Bartlett's test.

Appendix Table 2d. Effect of time of sampling on number of ventral gill rakers in sockeye salmon collected in 1958–60.

Year and area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
	1958									
Alaska Peninsula										
Chignik R.	7/1	5_2	23.125	72	0.646	0.094	1.061	4.292[a]	1,85	0.043
	7/31	5_2	23.600	15	0.686	0.214				
"	7/1	6_3	23.484	31	0.923	0.173	1.525	3.428	1,83	0.065
	7/31	6_3	23.130	54	0.606	0.106				
Kodiak Island										
Karluk R.	6/26	5_3	22.527	55	0.957	0.132	1.759	2.243	1,72	0.140
	8/31	5_3	22.895	19	0.544	0.169				
"	6/26	6_4	22.419	43	0.869	0.142	1.321	0.115	1,69	0.730
	8/31	6_4	22.500	28	1.148	0.202				
Bristol Bay										
Naknek R.	7/9	5_3	22.775	40	0.846	0.146	0.568[c]	0.223	2,67	0.807
	7/13	5_3	22.625	16	0.513	0.179				
	7/19	5_3	22.643	14	0.862	0.248				
Kvichak R.	7/10	5_3	22.973	37	0.639	0.132	2.285[c]	1.960	2,176	0.166
	7/16	5_3	23.214	42	0.905	0.147				
	7/24	5_3	22.870	100	0.983	0.99				
"	7/10	6_3	23.373	67	0.951	0.119	0.115[c]	3.177[a]	2,154	0.044
	7/16	6_3	23.179	39	0.940	0.115				
	7/24	6_3	22.922	51	0.874	0.131				
			$C = -2 \sum \ln P_i = 26.589$[a]							
	1959									
Alaska Peninsula										
Chignik R.	6/29	6_3	23.222	81	1.025	0.114	1.118	0.004	1,117	0.967
	8/2	6_3	23.211	38	1.144	0.173				
Bristol Bay										
Kvichak R.	7/9	5_3	23.000	190	0.825	0.063	9.042[c]	7.230[b]	2,346	0.001
	7/14	5_3	23.013	75	0.716	0.100				
	7/26	5_3	22.548	84	1.311	0.126				
			$C = -2 \sum \ln P_i = 13.903$[b]							
	1960									
Bristol Bay										
Kvichak R.	7/2	4_2	23.089	101	1.002	0.100	1.020[c]	0.896	2,295	0.422
	7/8	4_2	23.064	109	0.931	0.089				
	7/21	4_2	23.239	88	0.850	0.100				

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

[c] Bartlett's test.

APPENDIX TABLE 2e. Effect of time of sampling on total number of gill rakers in sockeye salmon collected in 1958–60.

Year and area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
	1958									
Alaska Peninsula										
Chignik R.	7/1	5_2	37.458	72	1.338	0.136	1.543	0.639	1,85	0.430
	7/31	5_2	37.733	15	2.064	0.117				
”	7/1	6_3	37.806	31	1.427	0.214	1.204	4.323[a]	1,83	0.043
	7/31	6_3	37.278	54	1.185	0.148				
Kodiak Island										
Karluk R.	6/26	5_3	36.418	55	1.933	0.187	1.141	4.132[a]	1,72	0.047
	8/31	5_3	37.158	19	1.694	0.299				
”	6/26	6_4	36.442	43	1.824	0.206	1.131	0.216	1,69	0.640
	8/31	6_4	36.286	28	2.063	0.271				
Bristol Bay										
Naknek R.	7/9	5_3	36.575	40	2.097	0.229	4.866[c]	0.338	1,67	0.560
	7/13	5_3	36.438	16	0.927	0.241				
	7/19	5_3	36.214	14	3.108	0.471				
Kvichak R.	7/10	5_3	37.162	37	1.642	0.211	1.010[c]	2.378	2,176	0.097
	7/16	5_3	37.500	42	2.207	0.229				
	7/24	5_3	36.930	100	2.126	0.146				
”	7/10	6_3	37.672	67	1.982	0.172	0.179[c]	2.629	2,154	0.079
	7/16	6_3	37.590	39	2.090	0.232				
	7/24	6_3	37.098	51	1.850	0.191				
			$C = -2 \sum \ln P_i = 25.891$[a]							
	1959									
Alaska Peninsula										
Chignik R.	6/29	6_3	37.531	81	2.152	0.161	1.020	0.028	1,117	0.857
	8/2	6_3	37.579	38	2.196	0.241				
Bristol Bay										
Kvichak R.	7/9	5_3	37.384	190	1.846	0.100	7.476[a,c]	17.365[b]	2,346	0.001
	7/14	5_3	37.320	75	1.572	0.021				
	7/26	5_3	36.321	84	2.775	0.182				
			$C = -2 \sum \ln P_i = 14.124$[b]							
	1960									
Bristol Bay										
Kvichak R.	7/2	4_2	37.396	101	2.243	0.148	0.660	1.175	2,295	0.312
	7/8	4_2	37.222	109	1.896	0.130				
	7/21	4_2	37.534	88	2.114	0.155				

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

[c] Bartlett's test.

Appendix Table 2f. Effect of time sampling on number of pectoral fin rays in sockeye salmon collected in 1958–60.

							F-values			
Year and area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
	1958									
Alaska Peninsula										
Chignik R.	7/1	5_2	16.181	72	0.235	0.574	1.372	0.021	1,85	0.880
	7/31	5_2	16.200	15	0.171	0.107				
"	7/1	6_3	16.290	31	0.231	0.083	1.185	2.459	1,83	0.123
	7/31	6_3	16.463	54	0.253	0.069				
Kodiak Island										
Karluk R.	6/26	5_3	16.315	54	0.258	0.069	1.670	7.137[b]	1,72	0.009
	8/31	5_3	16.700	20	0.437					
"	6/26	6_4	16.372	43	0.238	0.074	2.333[a]	1.252	1,69	0.267
	8/31	6_4	16.536	28	0.556	0.141				
Bristol Bay										
	7/9	5_3	16.359	39	0.290	0.086				
Naknek R.	7/13	5_3	16.313	16	0.360	0.150	1.463[c]	0.314	2,66	0.884
	7/19	5_3	16.214	14	0.492	0.188				
	7/10	5_3	16.405	37	0.247	0.083				
Kvichak R.	7/16	5_3	16.439	41	0.325	0.089	2.253[c]	1.855	2,176	0.288
	7/24	5_3	16.257	101	0.373	0.061				
	7/10	6_3	16.397	68	0.363	0.073				
"	7/16	6_3	16.436	39	0.463	0.109	2.570[c]	0.069	2,155	0.933
	7/24	6_3	16.392	51	0.284	0.075				
			$C = -2 \sum \ln P_i = 19.384$							
	1959									
Alaska Peninsula										
Chignik R.	6/29	6_3	16.220	82	0.322	0.063	1.267	2.287	1,118	0.134
	8/2	6_3	16.395	38	0.408	0.105				
Bristol Bay										
	7/9	5_3	16.414	191	0.360	0.045				
Kvichak R.	7/14	5_3	16.320	75	0.383	0.071	0.906[c]	5.074[b]	2,347	0.007
	7/26	5_3	16.167	84	0.309	0.063				
			$C = -2 \sum \ln P_i = 13.944$							
	1960									
Alaska Peninsula										
	7/2	4_2	16.436	101	0.368	0.063				
Kvichak R.	7/8	4_2	16.431	109	0.359	0.055	0.069[c]	0.005	2,298	0.990
	7/21	4_2	16.440	91	0.382	0.063				

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

[c] Bartlett's test.

Appendix Table 2g. Effect of time of sampling on number of anal fin rays in sockeye salmon collected in 1958–60.

							F-values			
Year and area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
	1958									
Alaska Peninsula										
Chignik R.	7/1	5_2	18.123	73	0.304	0.065	4.476[b]	0.010	1,85	0.925
	7/31	5_2	18.143	14	1.362	0.312				
"	7/1	6_3	18.484	31	0.390	0.112	1.076	0.178	1,83	0.675
	7/31	6_3	18.426	54	0.262	0.082				
Kodiak Island										
Karluk R.	6/26	5_3	18.091	55	0.306	0.075	1.550	7.015[b]	1,73	0.010
	8/31	5_3	18.500	20	0.474	0.154				
"	6/26	6_4	17.930	43	0.352	0.96	1.356	10.510[b]	1,69	0.003
	8/31	6_4	18.429	28	0.487	0.131				
Bristol Bay										
Naknek R.	7/9	5_3	18.308	39	0.429	0.105	9.950[b,c]	3.413[a]	2,66	0.041
	7/13	5_3	17.938	16	0.060	0.062				
	7/19	5_3	18.500	14	0.577	0.203				
Kvichak R.	7/10	5_3	18.270	37	0.481	0.114	2.380[c]	0.964	2,176	0.398
	7/16	5_3	18.381	42	0.390	0.096				
	7/24	5_3	18.200	100	0.556	0.075				
"	7/10	6_3	18.136	66	0.428	0.081	4.034[c]	1.267	2,151	0.292
	7/16	6_3	18.324	37	0.614	0.129				
	7/24	6_3	18.294	51	0.332	0.081				
			$C = -2 \sum \ln P_i = 32.464$[b]							
	1959									
Alaska Peninsula										
Chignik R.	6/29	6_3	18.173	81	0.320	0.063	1.561	0.416	1,117	0.517
	8/2	6_3	18.105	38	0.205	0.071				
Bristol Bay										
Kvichak R.	7/9	5_3	18.016	190	0.396	0.045	1.421[c]	0.278	2,344	0.837
	7/14	5_3	18.081	74	0.486	0.077				
	7/26	5_3	18.048	83	0.461	0.077				
			$C = -2 \sum \ln P_i = 1.675$							
	1960									
Bristol Bay										
Kvichak R.	7/2	4_2	18.287	101	0.527	0.071	1.425[c]	0.120	2,297	0.788
	7/8	4_2	18.303	109	0.417	0.063				
	7/21	4_2	18.256	90	0.426	0.071				

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

[c] Bartlett's test.

Appendix Table 3a. Effect of freshwater age on number of scales along the lateral line in sockeye salmon collected in 1957-58.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
Alaska Peninsula										
Chignik R.	7/26, 27, 28/57	5_2	131.317	60	4.458	0.272	1.792	2.011	1,143	0.161
	7/1, 31/58	6_3	130.882	85	2.488	0.170				
Kodiak Island										
Karluk R.	6/20/57	5_3	129.576	33	2.312	0.264	2.131	1.201	1,74	0.277
	6/26/58	6_4	130.070	43	4.928	0.339				
Bristol Bay										
Naknek R.	7/3, 5, 11, 12, 25/57	5_2	129.937	127	3.778	0.173	1.993	0.434	1,143	0.510
	7/9/58	6_3	130.278	18	7.529	0.646				
Egegik R.	7/13/57	5_2	130.176	17	2.062	0.348	1.354	0.011	1,69	0.915
	7/7/58	6_3	130.130	54	2.792	0.228				
Ugashik R.	7/19/57	4_2	130.933	30	4.069	0.369	1.472	0.292	1,101	0.587
	7/16/58	5_3	130.726	73	2.764	0.195				
Kvichak R.	7/9, 10/57	5_2	130.901	101	2.760	0.164	1.777	13.235[b]	1,257	0.001
	7/10, 16, 24/58	6_3	131.835	158	4.904	0.176				

$C = -2 \sum \ln P_i = 22.626^a$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 3b. Effect of freshwater age on number of vertebrae in sockeye salmon collected in 1957-58.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
Alaska Peninsula										
Chignik R.	7/26, 27, 28/57	5_2	67.508	59	0.879	0.122	1.231	1.832	1,142	0.179
	7/1, 31/58	6_3	67.306	85	0.714	0.089				
Kodiak Island										
Karluk R.	6/20/57	5_3	67.030	33	0.594	0.134	1.082	0.002	1,74	0.980
	6/26/58	6_4	67.023	43	0.643	0.122				
Bristol Bay										
Naknek R.	7/3, 5, 11, 12, 25/57	5_2	67.050	121	0.777	0.077	1.665	0.969	1,137	0.330
	7/9/58	6_3	67.278	18	1.294	0.268				
Egegik R.	7/13/57	5_2	67.412	17	0.438	0.161	1.317	1.891	1,68	0.173
	7/7/58	6_3	67.132	53	0.577	0.105				
Ugashik R.	7/19/57	4_2	67.400	30	0.655	0.148	1.011	0.064	1,100	0.793
	7/16/58	5_3	67.444	72	0.648	0.095				
Kvichak R.	7/9, 10/57	5_2	67.340	100	0.616	0.077	1.432	21.530[b]	1,252	0.001
	7/10, 16, 24/58	6_3	67.864	154	0.882	0.077				

$C = -2 \sum \ln P_i = 23.487^a$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 3c. Effect of freshwater age on position of the first haemal arch in sockeye salmon collected in 1957–58.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/26, 27, 28/57	5_2	34.814	59	0.534	0.095	1.360	2.210	1,142	0.140
	7/1, 31/58	6_3	34.612	85	0.726	0.089				
Kodiak Island										
Karluk R.	6/20/57	5_3	34.515	33	0.531	0.126	1.525	0.706	1,74	0.408
	6/26/58	6_4	34.674	43	0.810	0.138				
Bristol Bay										
Naknek R.	7/3, 5, 11, 12, 25/57	5_2	34.393	122	0.711	0.077	1.494	2.757	1,137	0.099
	7/9/58	6_3	34.765	17	1.062	0.248				
Egegik R.	7/13/57	5_2	34.706	17	0.625	0.192	1.003	2.116	1,69	0.151
	7/7/58	6_3	34.389	54	0.623	0.110				
Ugashik R.	7/19/57	4_2	34.633	30	0.586	0.141	1.034	0.003	1,100	0.970
	7/16/58	5_3	34.625	72	0.606	0.089				
Kvichak R.	7/9, 10/57	5_2	34.752	101	0.610	0.077	1.182	4.707[a]	1,254	0.035
	7/10, 16, 24/58	6_3	34.981	155	0.721	0.071				

$$C = -2 \sum \ln P_i = 20.897$$

[a] Significant at 5-percent level.

Appendix Table 3d. Effect of freshwater age on number of ventral gill rakers in sockeye salmon collected in 1957–58.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/26, 27, 28/57	5_2	23.400	60	0.678	0.105	1.088	0.976	1,143	0.327
	7/1, 31/58	6_3	23.259	85	0.738	0.095				
Kodiak Island										
Karluk R.	6/20/57	5_3	22.485	33	1.188	0.190	1.386	0.083	1,74	0.772
	6/26/58	6_4	22.419	43	0.857	0.141				
Bristol Bay										
Naknek R.	7/3, 5, 11, 12, 25/57	5_2	22.816	125	0.895	0.084	1.183	1.093	1,141	0.297
	7/9/58	6_3	23.000	18	1.059	0.243				
Egegik R.	7/13/57	5_2	22.750	16	0.467	0.170	2.302	0.191	1,68	0.659
	7/7/58	6_3	22.630	54	1.075	0.141				
Ugashik R.	7/19/57	4_2	22.967	30	1.276	0.205	1.482	0.291	1,101	0.586
	7/16/58	5_3	23.082	73	0.861	0.110				
Kvichak R.	7/9, 10/57	5_2	23.079	101	0.650	0.077	1.469	0.722	1,256	0.403
	7/10, 16, 24/58	6_3	23.178	157	0.955	0.077				

$$C = -2 \sum \ln P_i = 8.902$$

Appendix Table 3e. Effect of freshwater age on total number of gill rakers in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/26, 27, 28/57	5_2	37.667	60	1.746	0.170	1.322	0.901	1,143	0.348
	7/1, 31/58	6_3	37.470	85	1.321	0.126				
Kodiak Island										
Karluk R.	6/20/57	5_3	36.364	33	2.688	0.285	1.466	0.052	1,74	0.817
	6/26/58	6_4	36.442	43	1.833	0.207				
Bristol Bay										
Naknek R.	7/3, 5, 11, 12, 25/57	5_2	36.664	125	1.855	0.122	1.110	2.139	1,141	0.147
	7/9/58	6_3	37.167	18	2.059	0.338				
Egegik R.	7/13/57	5_2	37.125	16	1.333	0.288	1.515	0.075	1,68	0.783
	7/7/58	6_3	37.018	54	2.019	0.192				
Ugashik R.	7/19/57	4_2	37.366	30	2.310	0.277	1.289	0.072	1,101	0.788
	7/16/58	5_3	37.288	73	1.792	0.155				
Kvichak R.	7/9, 10/57	5_2	37.317	101	1.580	0.126	1.270	0.733	1,256	0.397
	7/10, 16, 24/58	6_3	37.465	157	2.006	0.114				

$C = -2 \sum \ln P_i = 9.163$

Appendix Table 3f. Effect of freshwater age on number of pectoral fin rays in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/26, 27, 28/57	5_2	16.350	60	0.373	0.077	1.567	0.299	1,143	0.582
	7/1, 31/58	6_3	16.400	85	0.238	0.055				
Kodiak Island										
Karluk R.	6/20/57	5_3	16.636	33	0.312	0.095	1.191	4.902[a]	1,74	0.029
	6/26/58	6_4	16.372	43	0.262	0.077				
Bristol Bay										
Naknek R.	7/3, 5, 11, 12, 25/57	5_2	16.323	127	0.317	0.045	1.669	1.466	1,143	0.238
	7/9/58	6_3	16.500	18	0.529	0.170				
Egegik R.	7/13/57	5_2	16.706	17	0.375	0.148	1.531	1.069	1,69	0.305
	7/7/58	6_3	16.556	54	0.245	0.063				
Ugashik R.	7/19/57	4_2	16.533	30	0.345	0.110	1.241	0.480	1,101	0.487
	7/16/58	5_3	16.452	73	0.278	0.063				
Kvichak R.	7/9, 10/57	5_2	16.604	101	0.300	0.055	1.190	7.264[b]	1,257	0.008
	7/10, 16, 24/58	6_3	16.405	158	0.357	0.045				

$C = -2 \sum \ln P_i = 24.505$[a]

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 3g. Effect of freshwater age on number of anal fin rays in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/26, 27, 28/57	5_2	18.150	60	0.441	0.084	1.195	7.838[b]	1,143	0.006
	7/1, 31/58	6_3	18.447	85	0.369	0.063				
Kodiak Island										
Karluk R.	6/20/57	5_3	18.062	32	0.322	0.318	1.109	0.001	1,73	0.999
	6/26/58	6_4	17.930	43	0.357	0.089				
Bristol Bay										
Naknek R.	7/3, 5, 11, 12, 25/57	5_2	17.960	126	0.424	0.055	1.623	21.400[b]	1,141	0.001
	7/9/58	6_3	18.765	17	0.688	0.200				
Egegik R.	7/13/57	5_2	17.765	17	0.312	0.134	1.538	5.765[a]	1,68	0.021
	7/7/58	6_3	18.208	53	0.480	0.095				
Ugashik R.	7/19/57	4_2	18.067	30	0.276	0.095	1.206	0.057	1,101	0.811
	7/16/58	5_3	18.096	73	0.333	0.063				
Kvichak R.	7/9, 10/57	5_2	18.010	101	0.290	0.055	1.531	8.008[b]	1,253	0.005
	7/10, 16, 24/58	6_3	18.234	154	0.444	0.055				

$C = -2 \sum \ln P_i = 42.792$[b]

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 3h. Effect of freshwater age on number of scales along the lateral line in sockeye salmon collected in 1958–59.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
Alaska Peninsula										
Chignik R.	6/29, 8/2/59	6_3	130.975	120	4.378	0.190	1.466	0.067	1,207	0.790
	7/1, 31/58	5_2	131.046	88	2.986	0.185				
Kodiak Island										
Karluk R.	6/24/59	6_4	129.917	36	3.449	0.310	1.002	0.154	1,90	0.692
	6/26/58	5_3	130.073	55	3.441	0.252				
Red R.	6/25/59	6_4	131.467	15	3.407	0.476	1.997	0.010	1,55	0.920
	6/24/58	5_3	131.512	41	1.706	0.207				
Bristol Bay										
Naknek R.	7/2/59	6_4	131.214	14	6.646	0.689	1.244	1.627	1,82	0.205
	7/9, 13, 19/58	5_3	130.333	69	5.343	0.280				
Egegik R.	7/7/59	6_4	130.087	23	4.082	0.421	1.114	0.056	1,121	0.814
	7/7/58	5_3	130.192	99	3.565	0.191				
Ugashik R.	7/11/59	6_3	130.724	76	2.283	0.173	1.649	0.526	1,125	0.470
	7/16/58	5_2	130.500	50	3.765	0.277				
Kvichak R.	7/9, 14, 26/59	5_3	130.914	348	3.635	0.100	1.148	0.000	1,370	0.999
	7/24/58	4_2	130.913	23	4.174	0.436				
Wood R.	6/29/59	5_3	130.700	20	4.116	0.454	1.246	0.424	1,141	0.515
	7/5/58	4_2	130.410	122	3.302	0.165				

$$C = -2 \sum \ln P_i = 7.795$$

Appendix Table 3i. Effect of freshwater age on number of vertebrae in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	*N*	Vari ance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula										
Chignik R.	6/29, 8/2/59	6_3	67.331	118	0.890	0.089	1.301	0.784	1,204	0.384
	7/1, 31/58	5_2	67.218	87	0.684	0.089				
Kodiak Island										
Karluk R.	6/24/59	6_4	67.086	35	0.785	0.148	1.443	0.663	1,88	0.422
	6/26/58	5_3	66.944	54	0.544	0.101				
Red R.	6/25/59	6_4	67.800	15	0.743	0.224	1.830	0.964	1,53	0.330
	6/24/58	5_3	67.590	39	0.406	0.102				
Bristol Bay										
Naknek R.	7/2/59	6_4	67.462	13	0.933	0.268	1.308	0.189	1,81	0.660
	7/9, 13, 19/58	5_3	67.319	69	1.220	0.134				
Egegik R.	7/7/59	6_4	67.174	23	0.786	0.184	1.414	0.003	1,119	0.970
	7/7/58	5_3	67.165	97	0.556	0.076				
Ugashik R.	7/11/59	6_3	67.273	77	0.411	0.071	2.433[a]	2.948	1,124	0.087
	7/16/58	5_2	67.021	48	1.000	0.146				
Kvichak R.	7/9, 14, 26/59	5_3	67.418	342	0.784	0.045	1.262	0.603	1,364	0.442
	7/24/58	4_2	67.565	23	0.621	0.168				
Wood R.	6/29/59	5_3	67.048	21	0.850	0.200	1.358	1.113	1,140	0.295
	7/5/58	4_2	67.250	120	0.626	0.073				

$$C = -2 \sum \ln P_i = 15.707$$

[a] Significant at 1-percent level.

Appendix Table 3j. Effect of freshwater age on position of first haemal arch in sockeye salmon collected in 1958–59.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
Alaska Peninsula										
Chignik R.	6/29, 8/2/59	6_3	34.542	118	0.661	0.077	1.143	0.032	1,204	0.854
	7/1, 31/58	5_2	34.563	87	0.668	0.088				
Kodiak Island										
Karluk R.	6/24/59	6_4	34.694	36	1.246	0.187	1.598	3.449	1,90	0.064
	6/26/58	5_3	34.309	55	0.736	0.117				
Red R.	6/25/59	6_4	34.667	15	0.521	0.187	1.626	0.001	1,55	0.999
	6/24/58	5_3	34.658	41	0.530	0.115				
Bristol Bay										
Naknek R.	7/2/59	6_4	34.929	14	0.685	0.221	1.857	1.014	1,83	0.317
	7/9, 13, 19/58	5_3	34.643	70	0.986	0.119				
Egegik R.	7/7/59	6_4	34.391	23	0.614	0.164	1.228	1.570	1,119	0.212
	7/7/58	5_3	34.639	97	0.754	0.089				
Ugạshik R.	7/11/59	6_3	34.610	77	0.715	0.095	1.474	2.576	1,126	0.112
	7/16/58	5_2	34.380	50	0.485	0.100				
Kvichak R.	7/9, 14, 26/59	5_3	34.690	345	0.703	0.045	1.010	0.570	1,367	0.455
	7/24/58	4_2	34.826	23	0.696	0.178				
Wood R.	6/29/59	5_3	34.238	21	0.690	0.182	2.467[a]	0.012	1,140	0.920
	7/5/58	4_2	34.217	120	0.675	0.075				

$$C = -2 \sum \ln P_i = 17.336$$

[a] Significant at 1-percent level.

Appendix Table 3k. Effect of freshwater age on number of ventral gill rakers in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula										
Chignik R.	6/29, 8/2/59	6_3	23.218	119	1.054	0.055	1.554[a]	0.007	1,205	0.945
	7/1, 31/58	5_2	23.207	87	0.678	0.089				
Kodiak Island										
Karluk R.	6/24/59	6_4	22.556	36	0.883	0.155	1.085	0.019	1,90	0.883
	6/26/58	5_3	22.527	55	0.958	0.133				
Red R.	6/25/59	6_4	22.867	15	0.550	0.192	1.022	0.498	1,55	0.483
	6/24/58	5_3	22.707	41	0.562	0.119				
Bristol Bay										
Naknek R.	7/2/59	6_4	23.286	14	0.685	0.221	1.106	5.109[a]	1,83	0.025
	7/9, 13, 19/58	5_3	22.714	70	0.758	0.105				
Egegik R.	7/7/59	6_4	22.609	23	1.341	0.241	1.461	2.582	1,121	0.112
	7/7/58	5_3	22.980	99	0.918	0.096				
Ugashik R.	7/11/59	6_3	22.923	78	1.033	0.114	1.266	2.463	1,127	0.120
	7/16/58	5_2	23.200	50	0.816	0.129				
Kvichak R.	7/9, 14, 26/59	5_3	22.894	349	0.951	0.055	1.072	0.542	1,371	0.465
	7/24/58	4_2	22.739	23	1.020	0.215				
Wood R.	6/29/59	5_3	22.667	21	0.835	0.200	1.187	1.671	1,142	0.197
	7/5/58	4_2	22.967	122	0.991	0.090				

$$C = -2 \sum \ln P_i = 22.595$$

[a] Significant at 5-percent level.

Appendix Table 31. Effect of freshwater age on total number of gill rakers in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula										
Chignik R.	6/29, 8/2/59	6_3	37.546	119	2.148	0.134	1.469	0.044	1,205	0.830
	7/1, 31/58	5_2	37.506	87	1.462	0.130				
Kodiak Island										
Karluk R.	6/24/59	6_4	36.472	36	2.257	0.251	1.179	0.031	1,90	0.852
	6/26/58	5_3	36.418	55	1.914	0.188				
Red R.	6/25/59	6_4	37.333	15	0.950	0.251	1.726	1.395	1,55	0.242
	6/24/58	5_3	36.902	41	1.640	0.202				
Bristol Bay										
Naknek R.	7/2/59	6_4	37.357	14	1.015	0.268	1.962	4.981[a]	1,83	0.025
	7/9, 13, 19/58	5_3	36.471	70	1.992	0.170				
Egegik R.	7/7/59	6_4	36.391	23	2.704	0.344	1.590	6.187[a]	1,121	0.016
	7/7/58	5_3	37.182	99	1.701	0.132				
Ugashik R.	7/11/59	6_3	37.090	78	2.550	0.182	1.684	3.410	1,127	0.065
	7/16/58	5_2	37.580	50	1.514	0.176				
Kvichak R.	7/9, 14, 26/59	5_3	37.115	349	2.199	0.077	1.060	0.814	1,371	0.372
	7/24/58	4_2	36.826	23	2.332	0.326				
Wood R.	6/29/59	5_3	36.857	21	1.530	0.270	1.242	0.864	1,142	0.358
	7/5/58	4_2	37.156	122	1.901	0.125				

$C = -2 \sum \ln P_i = 28.679$[a]

[a] Significant at 5-percent level.

Appendix Table 3m. Effect of freshwater age on number of pectoral fin rays in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula										
Chignik R.	6/29, 8/2/59	6_3	16.275	120	0.352	0.055	1.586[a]	1.407	1,206	0.238
	7/1, 31/58	5_2	16.184	87	0.222	0.050				
Kodiak Island										
Karluk R.	6/24/59	6_4	16.417	36	0.420	0.110	1.628	0.694	1,89	0.416
	6/26/58	5_3	16.315	54	0.258	0.070				
Red R.	6/25/59	6_4	16.800	15	0.171	0.105	1.766	2.337	1,55	0.134
	6/24/58	5_3	16.561	41	0.302	0.087				
Bristol Bay										
Naknek R.	7/2/59	6_4	16.357	14	0.246	0.134	1.374	0.053	1,82	0.816
	7/9, 13, 19/58	5_3	16.319	69	0.338	0.071				
Egegik R.	7/7/59	6_4	16.478	23	0.259	0.105	1.212	0.044	1,121	0.827
	7/7/58	5_3	16.505	99	0.314	0.057				
Ugashik R.	7/11/59	6_3	16.468	77	0.357	0.071	1.223	2.982	1,125	0.086
	7/16/58	5_2	16.286	49	0.292	0.078				
Kvichak R.	7/9, 14, 26/59	5_3	16.334	350	0.361	0.032	1.037	0.323	1,371	0.568
	7/24/58	4_2	16.409	22	0.348	0.129				
Wood R.	6/29/59	5_3	16.381	21	0.450	0.145	1.596	0.025	1,142	0.862
	7/5/58	4_2	16.361	122	0.282	0.048				

$$C = -2 \sum \ln P_i = 15.767$$

[a] Significant at 5-percent level.

Appendix Table 3n. Effect of freshwater age on number of anal fin rays in sockeye salmon collected in 1958–59.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	6/29, 8/2/59 7/1, 31/58	6_3 5_2	18.151 18.126	119 87	0.280 0.461	0.045 0.073	1.646[a]	0.087	1,205	0.767
Kodiak Island										
Karluk R.	6/24/59 6/26/58	6_4 5_3	18.139 18.091	36 53	0.523 0.306	0.118 0.077	1.709	0.128	1,90	0.718
Red R.	6/25/59 6/24/58	6_4 5_3	18.533 18.425	15 40	0.407 0.507	0.164 0.114	1.246	0.266	1,54	0.605
Bristol Bay										
Naknek R.	7/2/59 7/9, 13, 19/58	6_4 5_3	18.071 18.261	14 69	0.377 0.402	0.164 0.077	1.066	1.050	1,82	0.310
Egegik R.	7/7/59 7/7/58	6_4 5_3	18.043 18.144	23 97	0.500 0.479	0.148 0.071	1.044	0.391	1,119	0.531
Ugashik R.	7/11/59 7/16/58	6_3 5_2	18.179 17.900	78 50	0.331 0.418	0.063 0.092	1.263	6.521[a]	1,127	0.013
Kvichak R.	7/9, 14, 26/59 7/24/58	5_3 4_2	18.037 17.956	347 23	0.492 0.498	0.032 0.150	1.012	0.326	1,369	0.566
Wood R.	6/29/59 7/5/58	5_3 4_2	18.238 18.165	21 121	0.190 0.372	0.095 0.130	1.958	0.274	1,141	0.597

$C = -2 \sum \ln P_i = 16.662$

[a] Significant at 5-percent level.

Appendix Table 3o. Effect of freshwater age on meristic characters of sockeye salmon collected in the Wood River in 1959–60.

Character	Date	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Scales along lateral line	6/29/59 7/7/60	4_2 5_3	129.775 129.406	120 32	3.991 3.152	0.182 0.313	1.266	0.900	1,150	0.349
Total vertebrae	6/29/59 7/7/60	4_2 5_3	67.131 67.061	122 33	0.991 0.684	0.089 0.145	1.449	0.139	1,153	0.705
Position of first haemal arch	6/29/59 7/7/60	4_2 5_3	34.320 34.212	122 33	0.550 0.360	0.063 0.105	1.528	0.590	1,153	0.447
Ventral gill rakers	6/29/59 7/7/60	4_2 5_3	22.967 22.879	123 33	0.950 0.735	0.089 0.148	1.292	0.226	1,154	0.632
Total gill rakers	6/29/59 7/7/60	4_2 5_3	37.195 36.697	123 33	1.962 1.843	0.126 0.237	1.064	3.334	1,154	0.069
Pectoral fin rays	6/29/59 7/7/60	4_2 5_3	16.270 16.091	122 33	0.315 0.210	0.045 0.077	1.500	2.861	1,153	0.094
Anal fin rays	6/29/59 7/7/60	4_2 5_3	18.246 18.061	122 33	0.451 0.309	0.063 0.095	1.460	2.115	1,153	0.150

Appendix Table 4a. Effect of ocean age on number of scales along the lateral line in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Egegik R.	7/13/57	5_3	129.375	16	4.892	0.569	1.751	1.577	1,68	0.213
	7//7/58	6_3	130.963	54	2.794	0.228				
Ugashik R.	7/19/57	4_2	130.933	30	4.064	0.374	1.079	0.908	1,78	0.347
	7/16/58	5_2	130.500	50	3.765	0.277				
Kvichak R.	7/10/57	5_3	131.655	29	3.734	0.365	1.310	0.168	1,185	0.688
	7/10, 24/58	6_3	131.835	158	4.890	0.176				

$C = -2 \sum \ln P_i = 5.958$

Appendix Table 4b. Effect of ocean age on number of vertebrae in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance rotio	Analysis of variance	d. f.	*P*
Bristol Bay										
Egegik R.	7/13/57	5_3	67.125	16	0.650	0.208	1.124	0.001	1,67	0.999
	7/7/58	6_3	67.132	53	0.578	0.106				
Ugashik R.	7/19/57	4_2	67.400	30	0.662	0.151	1.510	3.025	1,76	0.085
	7/16/58	5_2	67.021	48	1.000	0.146				
Kvichak R.	7/10/57	5_3	67.793	29	1.098	0.198	1.253	0.133	1,181	0.715
	7/10, 24/58	6_3	67.864	154	0.877	0.076				

$C = -2 \sum \ln P_i = 5.603$

Appendix Table 4c. Effect of ocean age on position of the first haemal arch in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Egegik R.	7/13/57	5_3	34.500	16	0.533	0.189	1.162	0.254	1,68	0.615
	7/7/58	6_3	34.389	54	0.620	0.108				
Ugashik R.	7/19/57	4_2	34.633	30	0.585	0.142	1.206	2.303	1,78	0.135
	7/16/58	5_2	34.380	50	0.485	0.100				
Kvichak R.	7/10/57	5_3	34.897	29	0.882	0.178	1.224	0.232	1,182	0.646
	7/10, 24/58	6_3	34.981	155	0.720	0.068				

$C = -2 \sum \ln P_i = 5.851$

Appendix Table 4d. Effect of ocean age on number of ventral gill rakers in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Egegik R.	7/13/57	5_3	23.000	16	0.933	0.249	1.123	0.658	1,68	0.425
	7/7/58	6_3	22.630	54	1.048	0.170				
Ugashik R.	7/19/57	4_2	22.967	30	1.275	0.210	1.562	1.034	1,78	0.312
	7/16/58	5_2	23.200	50	0.816	0.129				
Kvichak R.	7/10/57	5_3	23.379	29	0.815	0.171	1.172	0.999	1,184	0.303
	7/10, 24/58	6_3	23.178	157	0.955	0.078				

$$C = -2 \sum \ln P_i = 6.429$$

Appendix Table 4e. Effect of ocean age on total number of gill rakers in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Egegik R.	7/13/57	5_3	37.188	16	2.029	0.368	1.005	0.174	1,68	0.684
	7/7/58	6_3	37.018	54	2.018	0.195				
Ugashik R.	7/19/57	4_2	37.367	30	1.964	0.260	1.298	0.508	1,78	0.455
	7/16/58	5_2	37.580	50	1.514	0.176				
Kvichak R.	7/10/57	5_3	37.793	29	1.741	0.079	1.152	1.340	1,184	0.269
	7/10, 24/58	6_3	37.465	157	2.001	0.113				

$$C = -2 \sum \ln P_i = 4.960$$

Appendix Table 4f. Effect of ocean age on number of pectoral fin rays in sockeye salmon collected in 1957–58.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Egegik R.	7/13/57	5_3	16.750	16	0.333	0.170	1.325	1.731	1,68	0.190
	7/7/58	6_3	16.556	54	0.252	0.069				
Ugashik R.	7/19/57	4_2	16.533	30	0.326	0.106	1.119	3.743	1,77	0.055
	7/16/58	5_2	16.286	49	0.292	0.078				
Kvichak R.	7/10/57	5_3	16.552	29	0.328	0.108	1.090	1.494	1,185	0.250
	7/10, 24/58	6_3	16.405	158	0.357	0.048				

$$C = -2 \sum \ln P_i = 11.895$$

Appendix Table 4g. Effect of ocean age on number of anal fin rays in sockeye salmon collected in 1957–58.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Bristol Bay										
Egegik R.	7/13/57	5_3	18.467	15	0.410	0.171	1.067	1.821	1,66	0.180
	7/7/58	6_3	18.207	53	0.437	0.092				
Ugashik R.	7/19/57	4_2	18.067	30	0.271	0.078	1.542	1.432	1,78	0.235
	7/16/58	5_2	17.900	50	0.418	0.092				
Kvichak R.	7/10/57	5_3	18.148	27	0.516	0.137	1.168	0.372	1,179	0.583
	7/10, 24/58	6_3	18.234	154	0.442	0.054				

$C = -2 \sum \ln P_i = 7.405$

Appendix Table 4h. Effect of ocean age on number of scales along the lateral line in sockeye salmon collected in 1958–59.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/31/58	5_3	131.158	19	1.807	0.308	2.423[a]	0.136	1,137	0.710
	6/29, 8/2/59	6_3	130.975	120	4.378	0.190				
Kodiak Island										
Karluk R.	6/26/58	5_3	130.073	55	3.441	0.250	1.434	3.317	1,69	0.087
	6/24/59	6_3	131.000	16	2.400	0.387				
"	6/26/58	6_4	130.070	43	4.924	0.338	4.428[b]	3.455	1,58	0.065
	6/24/59	7_4	131.118	17	1.112	0.255				
Red R.	6/24/58	5_3	131.512	41	1.706	0.207	1.876[a]	0.208	1,112	0.642
	6/25/59	6_3	131.658	73	3.200	0.210				
Bristol Bay										
Egegik R.	7/7/58	5_3	130.192	99	3.565	0.191	1.381	0.052	1,140	0.820
	7/7/59	6_3	130.116	43	2.581	0.245				
Ugashik R.	7/16/58	5_3	130.726	73	2.757	0.196	1.208	0.000	1,147	0.990
	7/11/59	6_3	130.724	76	2.283	0.173				
Wood R.	7/5/58	4_2	130.410	122	3.302	0.165	1.231	0.081	1,135	0.782
	6/29/59	5_2	130.267	15	4.064	0.521				

$C = -2 \sum \ln P_i = 12.831$

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 4i. Effect of ocean age on number of vertebrae in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula										
Chignik R.	7/31/58	5_3	67.526	19	0.930	0.221	1.045	0.700	1,135	0.410
	6/29, 8/2/59	6_3	67.331	118	0.890	0.089				
Kodiak Island										
Karluk R.	6/26/58	5_3	66.944	54	0.544	0.101	1.115	0.732	1,69	0.403
	6/24/59	6_3	67.118	17	0.488	0.170				
"	6/26/58	6_4	67.023	43	0.642	0.124	1.740	2.338	1,58	0.130
	6/24/59	7_4	67.353	17	0.369	0.148				
Red R.	6/24/58	5_3	67.590	39	0.406	0.102	1.818[a]	0.270	1,104	0.600
	6/25/59	6_3	67.507	67	0.738	0.105				
Bristol Bay										
Egegik R.	7/7/58	5_3	67.165	97	0.556	0.076	1.023	0.746	1,138	0.395
	7/7/59	6_3	67.047	43	0.569	0.114				
Ugashik R.	7/16/58	5_3	67.444	72	0.645	0.095	1.569	2.094	1,147	0.160
	7/11/59	6_3	67.273	77	0.411	0.071				
Wood R.	7/5/58	4_2	67.250	120	0.626	0.073	1.272	0.027	1,132	0.855
	6/29/59	5_2	67.214	14	0.492	0.187				

$$C = -2 \sum \ln P_i = 14.539$$

[a] Significant at 5-percent level.

Appendix Table 4j. Effect of ocean age on position of first haemal arch in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula										
Chignik R.	7/31/58	5_3	34.789	19	0.620	0.182	1.064	1.525	1,135	0.220
	6/29, 8/2/59	6_3	34.542	118	0.660	0.077				
Kodiak Island										
Karluk R.	6/26/58	5_3	34.309	55	0.736	0.117	1.886	0.383	1,70	0.535
	6/24/59	6_3	34.471	17	1.388	0.286				
"	6/26/58	6_4	34.674	43	0.796	0.138	3.038[a]	0.779	1,58	0.385
	6/24/59	7_4	34.471	17	0.262	0.122				
Red R.	6/24/58	5_3	34.658	41	0.530	0.115	1.868[a]	1.759	1,110	0.185
	6/25/59	6_3	34.423	73	0.990	0.118				
Bristol Bay										
Egegik R.	7/7/58	5_3	34.639	97	0.754	0.089	1.423	1.901	1,139	0.170
	7/7/59	6_3	34.432	44	0.530	0.110				
Ugashik R.	7/16/58	5_3	34.625	72	0.604	0.116	1.184	0.013	1,147	0.900
	7/11/59	6_3	34.610	77	0.715	0.095				
Wood R.	7/5/58	4_2	34.217	120	0.675	0.075	1.125	0.005	1,133	0.980
	6/29/59	5_2	34.200	15	0.600	0.200				

$$C = -2 \sum \ln P_i = 13.358$$

[a] Significant at 5-percent level.

Appendix Table 4k. Effect of ocean age on number of ventral gill rakers in sockeye salmon collected in 1958–59.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
Alaska Peninsula										
Chignik R.	7/31/58	5_3	23.105	19	1.099	0.241	1.043	0.198	1,136	0.652
	6/29, 8/2/59	6_3	23.218	119	1.054	0.095				
Kodiak Island										
Karluk R.	6/26/58	5_3	22.527	55	0.958	0.133	1.598	0.047	1,70	0.310
	6/24/59	6_3	22.824	17	1.531	0.300				
"	6/26/58	6_4	22.419	43	0.868	0.144	1.001	0.732	1,58	0.400
	6/24/59	7_4	22.647	17	0.869	0.226				
Red R.	6/24/58	5_3	22.707	41	0.562	0.119	1.740	0.233	1,113	0.626
	6/25/59	6_3	22.622	74	0.978	0.114				
Bristol Bay										
Egegik R.	7/7/58	5_3	22.980	99	0.918	0.096	1.032	2.820	1,141	0.152
	7/7/59	6_3	23.273	44	0.947	0.148				
Ugashik R.	7/16/58	5_3	23.082	73	0.854	0.109	1.210	1.008	1,149	0.318
	7/11/59	6_3	22.923	78	1.033	0.114				
Wood R.	7/5/58	4_2	22.967	122	0.991	0.090	1.136	0.128	1,136	0.716
	6/29/59	5_2	23.063	16	1.126	0.264				

$C = -2 \sum \ln P_i = 12.703$

Appendix Table 4l. Effect of ocean age on total number of gill rakers in sockeye salmon collected in 1958–59.

Area	Date	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
							Variance ratio	Analysis of variance		
Alaska Peninsula										
Chignik R.	7/31/58	5_3	37.526	19	2.263	0.345	1.054	0.003	1,136	0.996
	6/29, 8/2/59	6_3	37.546	119	2.148	0.134				
Kodiak Island										
Karluk R.	6/26/58	5_3	36.418	55	1.914	0.188	1.238	0.337	1,70	0.560
	6/24/59	6_3	36.647	17	2.369	0.373				
"	6/26/58	6_4	36.442	43	1.824	0.208	1.263	0.739	1,58	0.397
	6/24/59	7_4	36.765	17	1.444	0.292				
Red R.	6/24/58	5_3	36.902	41	1.640	0.202	1.278	0.473	1,113	0.494
	6/25/59	6_3	36.716	74	2.096	0.167				
Bristol Bay										
Egegik R.	7/7/58	5_3	37.182	99	1.701	0.132	1.055	4.812[a]	1,142	0.030
	7/7/59	6_3	37.705	44	1.794	0.202				
Ugashik R.	7/16/58	5_3	37.288	73	1.791	0.158	1.424	0.677	1,149	0.415
	7/11/59	6_3	37.090	78	2.550	0.182				
Wood R.	7/5/58	4_2	37.156	122	1.901	0.125	1.452	0.174	1,136	0.673
	6/29/59	5_2	37.313	16	2.760	0.416				

$C = -2 \sum \ln P_i = 13.990$

[a] Significant at 5-percent level.

Appendix Table 4m. Effect of ocean age on number of pectoral fin rays in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/31/58	5_3	16.421	19	0.480	0.158	1.364	0.948	1,137	0.335
	6/29, 8/2/59	6_3	16.275	120	0.352	0.055				
Kodiak Island										
Karluk R.	6/26/58	5_3	16.315	54	0.258	0.070	1.057	5.618[a]	1,69	0.018
	6/24/59	6_3	16.647	17	0.244	0.118				
”	6/26/58	6_4	16.372	43	0.239	0.075	1.232	8.312[b]	1,58	0.007
	6/24/59	7_4	16.765	17	0.194	0.105				
Red R.	6/24/58	5_3	16.561	41	0.302	0.087	1.094	0.004	1,113	0.998
	6/25/59	6_3	16.568	74	0.276	0.063				
Bristol Bay										
Egegik R.	7/7/58	5_3	16.505	99	0.314	0.057	1.096	0.541	1,140	0.465
	7/7/59	6_3	16.581	43	0.344	0.089				
Ugashik R.	7/16/58	5_3	16.452	73	0.279	0.062	1.280	0.028	1,148	0.858
	7/11/59	6_3	16.468	77	0.357	0.071				
Wood R.	7/5/58	4_2	16.361	122	0.282	0.048	1.418	0.931	1,136	0.340
	6/29/59	5_2	16.500	16	0.400	0.158				

$C = -2 \sum \ln P_i = 24.145$[a]

[a] Significant at 5-percent level.

[b] Significant at 1-percent level.

Appendix Table 4n. Effect of ocean age on number of anal fin rays in sockeye salmon collected in 1958–59.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula										
Chignik R.	7/31/58	5_3	18.421	19	0.591	0.176	2.096[a]	3.694	1,136	0.055
	6/29, 8/2/59	6_3	18.151	119	0.282	0.045				
Kodiak Island										
Karluk R.	6/26/58	5_3	18.091	53	0.306	0.158	1.595	0.027	1,70	0.860
	6/24/59	6_3	18.118	17	0.488	0.170				
”	6/26/58	6_4	17.930	43	0.352	0.092	1.688	3.848	1,58	0.054
	6/24/59	7_4	18.294	17	0.594	0.187				
Red R.	6/24/58	5_3	18.425	40	0.507	0.114	1.300	0.339	1,112	0.557
	6/25/59	6_3	18.500	74	0.390	0.071				
Bristol Bay										
Egegik R.	7/7/58	5_3	18.144	97	0.479	0.071	1.294	0.665	1,139	0.421
	7/7/59	6_3	18.045	44	0.370	0.089				
Ugashik R.	7/16/58	5_3	18.096	73	0.338	0.068	1.021	0.788	1,149	0.382
	7/11/59	6_3	18.179	78	0.331	0.063				
Wood R.	7/5/58	4_2	18.165	121	0.372	0.130	1.228	0.042	1,134	0.831
	6/29/59	5_2	18.200	15	0.457	0.173				

$C = -2 \sum \ln P_i = 17.136$

[a] Significant at 5-percent level.

Appendix Table 4o. Effect of ocean age on number of scales along the lateral line in sockeye salmon collected in 1959–60.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay										
Wood R.	6/29/59	4_2	129.775	120	3.991	0.182	1.087	4.559[a]	1,167	0.037
	7/7/60	5_2	130.490	49	3.672	0.274				
Egegik R.	7/7/59	5_3	130.292	96	2.756	0.170	1.391	0.285	1,109	0.590
	7/11/60	6_3	130.533	15	1.981	0.363				
Naknek R.	7/2/59	5_3	130.077	142	3.235	0.152	1.326	0.140	1,161	0.705
	7/7/60	6_3	130.238	21	4.290	0.452				
Ugashik R.	7/11/59	3_2	131.188	16	5.493	0.586	1.594	2.497	1,181	0.116
	7/14/60	4_2	130.401	167	3.446	0.145				

$C = -2 \sum \ln P_i = 12.656$

[a] Significant at 5-percent level.

Appendix Table 4p. Effect of ocean age on number of vertebrae in sockeye salmon collected in 1959–60.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay										
Wood R.	6/29/59	4_2	67.131	122	0.991	0.089	1.404	0.023	1,167	0.870
	7/7/60	5_2	67.106	47	0.706	0.122				
Egegik R.	7/7/59	5_3	67.156	96	0.702	0.084	2.096	2.551	1,108	0.113
	7/11/60	6_3	66.786	14	0.335	0.155				
Naknek R.	7/2/59	5_3	67.094	139	0.607	0.063	1.750	2.213	1,158	0.139
	7/7/60	6_3	66.810	21	1.062	0.224				
Ugashik R.	7/11/59	3_2	67.313	16	0.627	0.197	1.120	0.610	1,184	0.440
	7/14/60	4_2	67.159	170	0.560	0.055				

$C = -2 \sum \ln P_i = 10.228$

Appendix Table 4q. Effect of ocean age on position of first haemal arch in sockeye salmon collected in 1959–60.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay										
Wood R.	6/29/59	4_2	34.320	122	0.550	0.063	1.236	2.378	1,168	0.127
	7/7/60	5_2	34.521	48	0.680	0.118				
Egegik R.	7/7/59	5_3	34.552	96	0.839	0.095	1.305	0.195	1,109	0.654
	7/11/60	6_3	34.667	15	1.095	0.270				
Naknek R.	7/2/59	5_3	34.486	140	0.669	0.071	1.181	1.636	1,159	0.203
	7/7/60	6_3	34.238	21	0.790	0.195				
Ugashik R.	7/11/59	3_2	34.438	16	0.393	0.155	1.506	0.033	1,186	0.847
	7/14/60	4_2	34.401	172	0.592	0.055				

$C = -2 \sum \ln P_i = 8.498$

Appendix Table 4r. Effect of ocean age on number of ventral gill rakers in sockeye salmon collected in 1959–60.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Wood R.	6/29/59	4_2	22.967	123	0.950	0.089	1.250	0.708	1,170	0.407
	7/7/60	5_2	23.102	49	0.760	0.126				
Egegik R.	7/7/59	5_3	22.796	98	0.824	0.089	1.055	1.165	1,111	0.282
	7/11/60	6_3	23.067	15	0.781	0.228				
Naknek R.	7/2/59	5_3	22.972	142	0.964	0.084	1.066	0.247	1,161	0.617
	7/7/60	6_3	22.857	21	1.028	0.221				
Ugashik R.	7/11/59	3_2	23.000	16	0.533	0.182	1.681	0.082	1,186	0.771
	7/14/60	4_2	23.070	172	0.896	0.071				

$$C = -2 \sum \ln P_i = 5.816$$

Appendix Table 4s. Effect of ocean age on total number of gill rakers in sockeye salmon collected in 1959–60.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Wood R.	6/29/59	4_2	37.195	123	1.962	0.126	1.232	0.233	1,170	0.627
	7/7/60	5_2	37.306	49	1.592	0.179				
Egegik R.	7/7/59	5_3	37.265	98	1.805	0.134	2.522[a]	0.806	1,111	0.373
	7/11/60	6_3	37.600	15	1.707	0.338				
Naknek R.	7/2/59	5_3	36.972	142	1.843	0.114	1.491	1.164	1,161	0.281
	7/7/60	6_3	36.619	21	2.748	0.362				
Ugashik R.	7/11/59	3_2	37.188	16	1.093	0.261	1.542	0.061	1,186	0.801
	7/14/60	4_2	37.105	172	1.685	0.100				

$$C = -2 \sum \ln P_i = 5.888$$

[a] Significant at 5-percent level.

Appendix Table 4t. Effect of ocean age on number of pectoral fin rays in sockeye salmon collected in 1959–60.

							F-values			
Area	Date	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay										
Wood R.	6/29/59	4_2	16.270	122	0.315	0.045	1.452	0.155	1,169	0.692
	7/7/60	5_2	16.306	49	0.217	0.063				
Egegik R.	7/7/59	5_3	16.541	98	0.333	0.055	1.247	0.220	1,111	0.635
	7/11/60	6_3	16.467	15	0.267	0.134				
Naknek R.	7/2/59	5_3	16.193	140	0.301	0.045	1.292	1.233	1,159	0.269
	7/7/60	6_3	16.333	21	0.233	0.105				
Ugashik R.	7/11/59	3_2	16.250	16	0.200	0.110	1.540	0.829	1,185	0.368
	7/14/60	4_2	16.380	171	0.308	0.045				

$$C = -2 \sum \ln P_i = 6.270$$

Appendix Table 4u. Effect of ocean age on number of anal fin rays in sockeye salmon collected in 1959–60.

							F-values			
Area	Date	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay										
Wood R.	6/29/59	4_2	18.246	122	0.451	0.063	1.061	0.777	1,168	0.384
	7/7/60	5_2	18.146	48	0.425	0.095				
Egegik R.	7/7/59	5_3	18.010	97	0.469	0.071	1.096	0.003	1,110	0.960
	7/11/60	6_3	18.000	15	0.428	0.167				
Naknek R.	7/2/59	5_3	18.121	141	0.407	0.055	1.101	0.236	1,160	0.625
	7/7/60	6_3	18.048	21	0.448	0.145				
Ugashik R.	7/11/59	3_2	18.250	16	0.333	0.145	1.303	0.094	1,186	0.756
	7/14/60	4_2	18.302	172	0.434	0.045				

$$C = -2 \sum \ln P_i = 3.495$$

Appendix Table 5a. Effect of year class on number of scales along the lateral line in sockeye salmon collected in 1955–58.

								F-values			
Area	Date	Year class	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	131.317	60	4.457	0.275	1.492	0.173	1,146	0.674
	7/1, 31/58	1953	5_2	131.046	88	2.986	0.185				
"	7/25, 27, 28/57	1951	6_3	130.986	74	3.055	0.205	1.229	0.156	1,157	0.687
	7/1, 31/58	1952	6_3	130.882	85	2.486	0.172				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	130.000	15	5.429	0.623	3.901[a]	0.783	2,100	0.465
	6/20/57	1952	5_3	129.576	33	2.314	0.269				
	6/26/58	1953	5_3	130.073	55	3.441	0.252				
"	9/7/56	1951	5_3	131.063	16	3.662	0.494	0.779[a]	2.221	2,101	0.125
	8/21, 9/9, 17/57	1952	5_3	130.103	68	3.551	0.230				
	8/31/58	1953	5_3	130.500	20	2.579	0.368				
"	6/16, 29/55	1949	6_4	129.553	38	3.713	0.317	2.438[a]	0.716	2,133	0.493
	6/22/56	1950	6_4	129.891	55	3.136	0.239				
	6/26/58	1952	6_4	130.070	43	4.924	0.338				
"	8/24/55	1949	6_4	130.889	18	2.576	0.389	2.679[a]	0.636	3,167	0.599
	9/7/56	1950	6_4	130.794	68	3.987	0.244				
	8/21, 9/9, 17/57	1951	6_4	130.351	57	2.803	0.222				
	8/31/58	1952	6_4	130.571	28	3.884	0.373				
Red R.	6/18/56	1951	5_3	131.290	31	3.280	0.331	4.110[a]	3.620[b]	2,127	0.032
	6/21/57	1952	5_3	130.672	58	2.821	0.222				
	6/24/58	1953	5_2	131.512	41	1.706	0.207				
Bristol Bay											
Egegik R.	7/17/56	1951	5_3	130.009	110	2.468	0.150	5.447[a]	1.517	2,222	0.245
	7/13/57	1952	5_3	129.370	16	4.917	0.573				
	7/7/58	1953	5_3	130.192	99	3.565	0.191				
"	7/17/56	1950	6_3	130.250	16	4.600	0.554	3.306[a]	0.158	2,173	0.858
	7/13/57	1951	6_3	130.377	106	4.294	0.202				
	7/7/58	1952	6_3	130.130	54	2.794	0.230				
Ugashik R.	7/19/57	1952	5_2	130.522	67	1.920	0.170	1.961[b]	1.503	1,115	0.224
	7/16/58	1953	5_2	130.500	50	3.765	0.277				
"	7/23/56	1951	5_3	129.743	35	3.844	0.336	1.424[a]	4.761[b]	2,135	0.011
	7/19/57	1952	5_3	129.900	30	2.783	0.310				
	7/16/58	1953	5_3	130.726	73	2.757	0.196				
Kvichak R.	7/13/56	1951	5_3	131.528	53	3.946	0.275	6.520[a,b]	0.105	2,258	0.900
	7/10/57	1952	5_3	131.655	29	3.734	0.365				
	7/10, 16, 24/58	1953	5_3	131.760	179	6.411	0.189				
"	7/13/56	1952	4_2	130.815	108	4.377	0.202	1.048	0.183	1,129	0.667
	7/24/58	1954	4_2	130.913	23	4.174	0.436				
Wood R.	7/11/56	1952	4_2	129.864	118	3.520	0.173	1.066	3.035	1,138	0.083
	7/5/58	1954	4_2	130.410	122	3.302	0.165				
"	7/11/56	1951	5_2	130.500	46	2.656	0.243	1.204[a]	3.912[b]	2,112	0.024
	7/17/57	1952	5_2	129.556	45	3.389	0.278				
	7/5/58	1953	5_2	130.375	24	2.332	0.318				

Continued . . .

Appendix Table 5a. Continued.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Naknek R.	7/6/56	1951	5_2	130.750	28	5.083	0.434	9.316[a,b]	2.448	3,203	0.069
	7/8/56	1951	5_2	130.471	34	4.802	0.381				
	7/3, 5, 11, 12, 25/57	1952	5_2	129.937	127	3.774	0.173				
	7/9/58	1953	5_2	131.056	18	7.820	0.678				
"	7/6/56	1951	5_3	131.471	17	6.890	0.656	1.289	3.129	1,84	0.080
	7/9, 13, 19/58	1953	5_3	130.333	69	5.343	0.280				
"	7/6/56	1950	6_3	130.237	38	4.618	0.353	4.197[a]	3.321[b]	3,415	0.021
	7/8/56	1950	6_3	129.897	39	6.683	0.419				
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	130.901	324	4.665	0.120				
	7/9/58	1952	6_3	130.278	18	7.506	0.664				

$$C = -2 \sum \ln P_i = 63.268^{b}$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

Appendix Table 5b. Effect of year class on number of vertebrae in sockeye salmon collected in 1955-58.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	67.508	59	0.875	0.123	1.278	3.914[b]	1,144	0.050
	7/1, 31/58	1953	5_2	67.218	87	0.684	0.089				
"	7/25, 27, 28/57	1951	6_3	67.197	71	0.589	0.992	1.213	0.695	1,154	0.414
	7/1, 31/58	1952	6_3	67.306	85	0.715	0.092				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	66.800	15	0.743	0.230	0.560[a]	0.469	2,99	0.635
	6/20/57	1952	5_3	67.030	33	0.592	0.136				
	6/26/58	1953	5_3	66.944	54	0.544	0.101				
"	9/7/56	1951	5_3	67.562	16	0.662	0.210	0.014[a]	0.643	2,98	0.533
	8/21, 9/9, 17/57	1952	5_3	67.303	66	0.676	0.102				
	8/31/58	1953	5_3	67.368	19	0.690	0.196				
"	6/16, 29/55	1949	6_4	67.053	38	0.754	0.143	0.306[a]	0.528	2,133	0.600
	6/22/56	1950	6_4	66.891	55	0.654	0.110				
	6/26/58	1952	6_4	67.023	43	0.642	0.124				

Continued . . .

Appendix Table 5b. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Karluk R.	8/24/55	1949	6_4	67.444	18	1.438	0.384	3.860[a]	0.092	3,167	0.964
	9/7/56	1950	6_4	67.373	67	0.753	0.107				
	8/21, 9/9, 17/57	1951	6_4	67.424	59	0.731	0.112				
	8/31/58	1952	6_4	67.333	27	0.769	0.169				
Red R.	6/18/56	1951	5_3	67.677	31	0.492	0.128	1.772[a]	1.801	2,123	0.198
	6/21/57	1952	5_3	67.393	56	0.606	0.104				
	6/24/58	1953	5_3	67.590	39	0.406	0.102				
Bristol Bay											
Egegik R.	7/17/56	1951	5_3	67.234	111	0.526	0.069	0.317[a]	0.307	2,221	0.740
	7/13/57	1952	5_3	67.125	16	0.650	0.208				
	7/7/58	1953	5_3	67.165	97	0.556	0.076				
"	7/17/56	1950	6_3	67.188	16	0.829	0.235	1.234[a]	1.562	2,171	0.237
	7/13/57	1951	6_3	67.371	105	0.736	0.084				
	7/7/58	1952	6_3	67.132	53	0.578	0.105				
Ugashik R.	7/19/57	1952	5_2	67.418	67	0.489	0.086	2.042[b]	6.284[b]	1,113	0.015
	7/16/58	1953	5_2	67.021	48	1.000	0.146				
"	7/23/56	1951	5_3	67.265	34	0.625	0.138	0.388[a]	1.054	2,133	0.364
	7/19/57	1952	5_3	67.233	30	0.530	0.135				
	7/16/58	1953	5_3	67.444	72	0.645	0.095				
Kvichak R.	7/13/56	1951	5_3	67.608	51	0.923	0.136	0.784[a]	1.289	2,251	0.286
	7/10/57	1952	5_3	67.793	29	1.098	0.195				
	7/10, 16, 24/58	1953	5_3	67.874	174	1.128	0.105				
"	7/13/56	1952	4_2	67.373	110	0.676	0.077	1.090	1.057	1,131	0.307
	7/24/58	1954	4_2	67.565	23	0.621	0.168				
Wood R.	7/11/56	1952	4_2	67.254	118	0.602	0.072	1.041	0.009	1,236	0.968
	7/5/58	1954	4_2	67.250	120	0.626	0.073				
"	7/11/56	1951	5_2	67.422	45	0.840	0.138	2.207[a]	2.040	2,109	0.156
	7/17/57	1952	5_2	67.091	44	0.550	0.113				
	7/5/58	1953	5_2	67.130	23	0.573	0.161				
Naknek R.	7/6/56	1951	5_2	67.407	27	0.943	0.190	2.337[a]	1.202	3,196	0.313
	7/8/56	1951	5_2	67.382	34	1.031	0.177				
	7/3, 5, 11, 12, 25/57	1952	5_2	67.050	121	0.781	0.080				
	7/9/58	1953	5_2	67.278	18	0.565	0.172				
"	7/6/56	1951	5_3	67.588	17	1.132	0.266	1.078	1.670	1,84	0.200
	7/9, 13, 19/58	1953	5_3	67.319	69	1.220	0.134				
"	7/6/56	1950	6_3	67.378	37	1.297	0.190	2.162[a]	0.764	3,399	0.515
	7/8/56	1950	6_3	67.410	39	1.248	0.181				
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	67.547	309	0.989	0.057				
	7/9/58	1952	6_3	67.278	18	1.271	0.2735				

$$C = -2 \sum \ln P_i = 43.674$$

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[a] Bartlett's test.

[b] Significant at 5-percent level.

Appendix Table 5c. Effect of year class on position of the first haemal arch in sockeye salmon collected in 1955–58.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	34.814	59	0.534	0.096	1.251	3.591	1,144	0.059
	7/1, 31/58	1953	5_2	34.563	87	0.668	0.088				
"	7/25, 27, 28/57	1951	6_3	34.417	72	1.007	0.119	1.405	1.746	1,155	0.189
	7/1, 31/58	1952	6_3	34.612	85	0.716	0.092				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	34.467	15	0.552	0.199	1.463[a]	0.752	2,100	0.478
	6/20/57	1952	5_3	34.515	33	0.508	0.126				
	6/26/58	1953	5_3	34.309	55	0.736	0.117				
"	9/7/56	1951	5_3	34.375	16	0.517	0.186	1.547[a]	0.065	2,98	0.938
	8/21, 9/9, 17/57	1952	5_3	34.439	66	0.865	0.115				
	8/31/58	1953	5_3	34.368	19	0.912	0.225				
"	6/16, 29/55	1949	6_4	34.718	39	0.524	0.117	2.842[a]	0.504	2,134	0.615
	6/22/56	1950	6_4	34.564	55	0.510	0.097				
	6/26/58	1952	6_4	34.674	43	0.796	0.138				
"	8/24/55	1949	6_4	34.778	18	0.771	0.213	0.333[a]	0.479	3,166	0.698
	9/7/56	1950	6_4	34.508	67	0.829	0.221				
	8/21, 9/9, 17/57	1951	6_4	34.596	57	0.745	0.115				
	8/31/58	1952	6_4	34.536	28	0.702	0.203				
Red R.	6/18/56	1951	5_3	34.806	31	0.828	0.166	1.761[a]	1.158	2,125	0.324
	6/21/57	1952	5_3	34.536	56	0.617	0.106				
	6/24/58	1953	5_3	34.658	41	0.530	0.115				
Bristol Bay											
Egegik R.	7/17/56	1951	5_3	34.568	111	0.466	0.065	5.952[a]	0.350	2,221	0.706
	7/13/57	1952	5_3	34.500	16	0.533	0.189				
	7/7/58	1953	5_3	34.639	97	0.754	0.089				
"	7/17/56	1950	6_3	34.375	16	1.317	0.296	2.010[a]	0.285	2,173	0.757
	7/13/57	1951	6_3	34.481	106	0.614	0.076				
	7/7/58	1952	6_3	34.389	54	0.620	0.108				
Ugashik R.	7/19/57	1952	5_2	34.761	67	0.609	0.095	1.254	7.482[b]	1,115	0.008
	7/16/58	1953	5_2	34.380	50	0.485	0.100				
"	7/23/56	1951	5_3	34.382	34	0.668	0.142	0.725[a]	2.164	2,133	0.134
	7/19/57	1952	5_3	34.800	30	0.786	0.165				
	7/16/58	1953	5_3	34.625	72	0.604	0.116				
Kvichak R.	7/13/56	1951	5_3	34.863	51	0.681	0.136	13.128[a,b]	0.083	2,255	0.920
	7/10/57	1952	5_3	34.897	29	0.882	0.177				
	7/10, 16, 24/58	1953	5_3	34.922	178	0.875	0.070				
"	7/13/56	1952	4_2	34.712	111	0.807	0.086	1.160	0.316	1,132	0.575
	7/24/58	1954	4_2	34.826	23	0.696	0.178				
Wood R.	7/11/56	1952	4_2	34.339	118	0.619	0.073	1.091	1.375	1,236	0.245
	7/5/58	1954	4_2	34.217	120	0.675	0.075				
"	7/11/56	1951	5_2	34.456	46	0.787	0.132	3.788[a]	0.067	2,110	0.935
	7/17/57	1952	5_2	34.409	44	0.433	0.099				
	7/5/58	1953	5_2	34.391	23	0.613	0.167				

Continued . . .

APPENDIX TABLE 5c. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Naknek R.	7/6/56	1951	5_2	34.654	26	0.635	0.156	0.376[a]	1.015	3,196	0.398
	7/8/56	1951	5_2	34.588	34	0.795	0.155				
	7/3, 5, 11, 12, 25/57	1952	5_2	34.393	122	0.703	0.076				
	7/9/58	1953	5_2	34.389	18	0.722	0.206				
"	7/6/56	1951	5_3	34.588	17	0.882	0.228	1.118	0.051	1,85	0.820
	7/9, 13, 19/58	1953	5_3	34.643	70	0.986	0.119				
"	7/6/56	1950	6_3	34.568	37	0.808	0.149	1.406[a]	0.675	3,404	0.572
	7/8/56	1950	6_3	34.447	38	0.794	0.147				
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	34.639	316	0.841	0.052				
	7/9/58	1952	6_3	34.765	17	1.066	0.258				

$$C = -2 \sum \ln P_i = 37.050$$

[a] Bartlett's test.

[b] Significant at 1-percent level.

APPENDIX TABLE 5d. Effect of year class on number of ventral gill rakers in sockeye salmon collected in 1955–58.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	23.400	60	0.685	0.108	1.010	1.946	1,145	0.197
	7/1, 31/58	1953	5_2	23.207	87	0.678	0.089				
"	7/25, 27, 28/57	1951	6_3	23.227	75	0.772	0.102	1.041	0.054	1,158	0.843
	7/1, 31/58	1952	6_3	23.259	85	0.742	0.094				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	22.533	15	0.552	0.199	2.207[a]	0.023	2,100	0.978
	6/20/57	1952	5_3	22.485	33	1.133	0.188				
	6/26/58	1953	5_3	22.527	55	0.958	0.133				
"	9/7/56	1951	5_3	22.312	16	1.295	0.294	1.491[a]	2.106	2,100	0.145
	8/21, 9/9, 17/57	1952	5_3	22.750	68	0.728	0.104				
	8/31/58	1953	5_3	22.895	19	0.544	0.174				
"	6/16, 29/55	1949	6_4	22.316	38	0.708	0.063	2.102[a]	0.770	2,133	0.472
	6/22/56	1950	6_4	22.364	55	0.569	0.103				
	6/26/58	1952	6_4	22.419	43	0.868	0.144				

Continued . . .

Appendix Table 5d. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	*F*-values		d. f.	P
								Variance ratio	Analysis of variance		
Karluk R.	8/24/55	1949	6_4	22.444	18	0.967	0.239	0.499[a]	1.131	3,169	0.345
	9/7/56	1950	6_4	22.609	69	0.918	0.116				
	8/21, 9/9, 17/57	1951	6_4	22.828	58	0.987	0.132				
	8/31/58	1952	6_4	22.500	28	1.148	0.206				
Red R.	6/18/56	1951	5_3	22.871	31	1.050	0.184	1.659[a]	0.636	2,127	0.537
	6/21/57	1952	5_3	22.914	58	0.922	0.127				
	6/24/58	1953	5_3	22.707	41	0.562	0.119				
Bristol Bay											
Egegik R.	7/17/56	1951	5_3	23.045	110	0.888	0.090	0.032[a]	0.126	2,222	0.884
	7/13/57	1952	5_3	23.000	16	0.933	0.249				
	7/7/58	1953	5_3	22.980	99	0.918	0.096				
"	7/17/56	1950	6_3	22.938	16	0.996	0.258	0.564[a]	2.129	2,173	0.136
	7/13/57	1951	6_3	22.962	106	0.894	0.092				
	7/7/58	1952	6_3	22.630	54	1.068	0.142				
Ugashik R.	7/19/57	1952	5_2	22.985	66	0.692	0.103	1.179	1.766	1,114	0.185
	7/16/58	1953	5_2	23.200	50	0.816	0.129				
"	7/23/56	1951	5_3	22.765	34	0.670	0.143	3.677[a]	1.293	2,134	0.287
	7/19/57	1952	5_3	23.000	30	1.310	0.213				
	7/16/58	1953	5_3	23.082	73	0.854	0.109				
Kvichak R.	7/13/56	1951	5_3	23.058	52	0.840	0.128	0.205[a]	2.368	2,257	0.097
	7/10/57	1952	5_3	23.379	29	0.815	0.171				
	7/10, 16, 24/58	1953	5_3	22.972	179	0.904	0.071				
"	7/13/56	1952	4_2	23.100	110	0.770	0.084	1.325	3.052	1,131	0.082
	7/24/58	1954	4_2	22.739	23	1.020	0.215				
Wood R.	7/11/56	1952	4_2	22.636	118	0.746	0.080	1.327	7.577[c]	1,238	0.007
	7/5/58	1954	4_2	22.967	122	0.991	0.090				
"	7/11/56	1951	5_2	23.089	45	1.219	0.166	5.678[a]	2.270	2,111	0.116
	7/17/57	1952	5_2	22.667	45	0.682	0.124				
	7/5/58	1953	5_2	22.833	24	0.667	0.170				
Naknek R.	7/6/56	1951	5_2	22.964	28	0.962	0.189	1.735[a]	1.077	3,201	0.370
	7/8/56	1951	5_2	23.029	34	0.636	0.139				
	7/3, 5, 11, 12, 25/57	1952	5_2	22.816	125	0.893	0.085				
	7/9/58	1953	5_2	22.500	18	0.971	0.239				
"	7/6/56	1951	5_3	23.125	16	0.517	0.186	1.467[a]	3.074	1,84	0.082
	7/9, 13, 19/58	1953	5_3	22.714	70	0.758	0.105				
"	7/6/56	1950	6_3	22.737	38	0.794	0.145	1.630[a]	1.416	3,413	0.257
	7/8/56	1950	6_3	23.026	39	1.078	0.168				
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	23.065	322	0.840	0.051				
	7/9/58	1952	6_3	23.000	18	1.059	0.246				

$$C = -2 \sum \ln P_i = 56.087^{b}$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5e. Effect of year class on total number of gill rakers in sockeye salmon collected in 1955–58.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	37.667	60	1.751	0.172	1.198	0.582	1,145	0.460
	7/1,31/58	1953	5_2	37.506	87	1.462	0.130				
"	7/25, 27, 28/57	1951	6_3	37.400	75	1.730	0.153	1.307	0.131	1,158	0.729
	7/1, 31/58	1952	6_3	37.471	85	1.324	0.126				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	36.533	15	2.114	0.389	4.091[a]	0.134	2,100	0.877
	6/20/57	1952	5_3	36.364	33	2.676	0.289				
	6/26/58	1953	5_3	36.418	55	1.914	0.188				
"	9/7/56	1951	5_3	36.438	16	2.529	0.411	0.812[a]	1.261	2,100	0.293
	8/21, 9/9, 17/57	1952	5_3	36.706	68	1.852	0.166				
	8/31/58	1953	5_3	37.158	19	1.695	0.307				
"	6/16, 29/55	1949	6_4	35.974	38	1.540	0.204	0.866[a]	1.419	2,131	0.265
	6/22/56	1950	6_4	36.189	53	1.387	0.163				
	6/26/58	1952	6_4	36.442	43	1.824	0.208				
"	8/24/55	1949	6_4	35.944	18	2.761	0.403	0.797[a]	1.549	3,168	0.228
	9/7/56	1950	6_4	36.412	68	2.007	0.173				
	8/21, 9/9, 17/57	1951	6_4	37.724	58	2.238	0.198				
	8/31/58	1952	6_4	36.286	28	2.064	0.276				
Red R.	6/18/56	1951	5_3	36.806	31	1.761	0.242	0.420[a]	0.492	2,127	0.622
	6/21/57	1952	5_3	37.086	58	1.974	0.186				
	6/24/58	1953	5_3	36.902	41	1.640	0.202				
Bristol Bay											
Egegik R.	7/17/56	1951	5_3	37.300	110	1.955	0.134	0.478[a]	0.210	2,222	0.817
	7/13/57	1952	5_3	37.188	16	2.029	0.368				
	7/7/58	1953	5_3	37.182	99	1.701	0.132				
"	7/17/56	1950	6_3	37.250	16	1.400	0.305	1.340[a]	0.340	2,173	0.713
	7/13/57	1951	6_3	37.189	106	1.719	0.128				
	7/7/58	1952	6_3	37.019	54	2.018	0.195				
Ugashik R.	7/19/57	1952	5_2	37.121	66	1.308	0.142	1.157	4.288[b]	1,114	0.044
	7/16/58	1953	5_2	37.580	50	1.514	0.176				
"	7/23/56	1951	5_3	36.765	34	1.700	0.227	3.700[a]	1.641	2,134	0.226
	7/19/57	1952	5_3	37.000	30	3.034	0.323				
	7/16/58	1953	5_3	37.288	73	1.791	0.158				
Kvichak R.	7/13/56	1951	5_3	37.346	52	1.956	0.196	0.189[a]	0.583	2,257	0.566
	7/10/57	1952	5_3	37.793	29	2.026	0.269				
	7/10, 16, 24/58	1953	5_3	37.112	179	2.077	0.108				
"	7/13/56	1952	4_2	37.391	110	1.396	0.113	1.670	3.907	1,131	0.051
	7/24/58	1954	4_2	36.826	23	2.332	0.326				
Wood R.	7/11/56	1952	4_2	36.500	118	1.842	0.125	1.032	13.778[c]	1,238	0.001
	7/5/58	1954	4_2	37.156	122	1.901	0.125				
"	7/11/56	1951	5_2	37.200	45	2.573	0.242	5.178[a]	2.408	2,111	0.097
	7/17/57	1952	5_2	36.578	45	1.431	0.180				
	7/5/58	1953	5_2	37.000	24	1.304	0.238				

Continued . . .

Appendix Table 5e. Continued.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Naknek R.	7/6/56	1951	5_2	37.143	28	2.275	0.290	5.030[a]	0.898	3,210	0.451
	7/8/56	1951	5_2	37.147	34	1.038	0.177				
	7/3, 5, 11, 12, 25/57	1952	5_2	36.627	134	1.890	0.119				
	7/9/58	1953	5_2	36.333	18	1.765	0.102				
"	7/6/56	1951	5_3	37.125	16	1.183	0.281	1.683	3.011	1,84	0.085
	7/9, 13, 19/58	1953	5_3	36.471	70	1.992	0.170				
"	7/6/56	1950	6_3	36.710	38	1.561	0.205	3.709[a]	2.618	3,413	0.082
	7/8/56	1950	6_3	37.231	39	2.498	0.256				
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	37.338	322	1.651	0.072				
	7/9/58	1952	6_3	37.167	18	2.029	0.346				

$C = -2 \sum \ln P_i = 58.865$[b]

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5f. Effect of year class on number of pectoral fin rays in sockeye salmon collected in 1955–58.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	16.350	60	0.367	0.091	1.656	3.490	1,145	0.068
	7/1, 31/58	1953	5_2	16.184	87	0.222	0.050				
"	7/25, 27, 28/57	1951	6_3	16.333	75	0.279	0.061	1.150	0.681	1,158	0.428
	7/1, 31/58	1952	6_3	16.400	85	0.243	0.054				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	16.533	15	0.267	0.138	0.258[a]	4.099[b]	2,99	0.021
	6/20/57	1952	5_3	16.636	33	0.301	0.097				
	6/26/58	1953	5_3	16.315	54	0.258	0.070				
"	9/7/56	1951	5_3	16.625	16	0.250	0.129	1.199[a]	2.056	2,101	0.153
	8/21, 9/9, 17/57	1952	5_3	16.426	68	0.338	0.071				
	8/31/58	1953	5_3	16.700	20	0.437	0.151				
"	6/16, 29/55	1949	6_4	16.316	38	0.330	0.093	1.409[a]	1.255	2,133	0.294
	6/22/56	1950	6_4	16.491	55	0.329	0.078				
	6/26/58	1952	6_4	16.372	43	0.239	0.075				

Continued . . .

Appendix Table 5f. Continued.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Karluk R.	8/24/55	1949	6_4	16.444	18	0.261	0.124	5.234[a]	1.021	3,169	0.395
	9/7/56	1950	6_4	16.551	69	0.398	0.077				
	8/21, 9/9, 17/57	1951	6_4	16.690	58	0.288	0.071				
	8/31/58	1952	6_4	16.536	28	0.554	0.141				
Red R.	6/18/56	1951	5_3	16.581	31	0.318	0.103	0.060[a]	0.027	2,127	0.974
	6/21/57	1952	5_3	16.551	58	0.322	0.075				
	6/24/58	1953	5_3	16.561	41	0.302	0.087				
Bristol Bay											
Egegik R.	7/17/56	1951	5_3	16.486	111	0.307	0.053	0.081[a]	1.577	2,223	0.236
	7/13/57	1952	5_3	16.750	16	0.333	0.149				
	7/7/58	1953	5_3	16.505	99	0.314	0.057				
”	7/17/56	1950	6_3	16.500	16	0.267	0.133	0.098[a]	0.002	2,173	0.999
	7/13/57	1951	6_3	16.396	106	0.270	0.050				
	7/7/58	1952	6_3	16.556	54	0.252	0.069				
Ugashik R.	7/19/57	1952	5_2	16.433	67	0.325	0.070	1.114	2.027	1,114	0.157
	7/16/58	1953	5_2	16.286	49	0.292	0.078				
”	7/23/56	1951	5_3	16.471	34	0.257	0.088	2.497[a]	0.972	2,134	0.395
	7/19/57	1952	5_3	16.300	30	0.424	0.121				
	7/16/58	1953	5_3	16.452	73	0.279	0.062				
Kvichak R.	7/13/56	1951	5_3	16.365	52	0.315	0.079	0.048[a]	1.868	2,257	0.204
	7/10/57	1952	5_3	16.552	29	0.328	0.108				
	7/10, 16, 24/58	1953	5_3	16.330	179	0.335	0.043				
”	7/13/56	1952	4_2	16.518	110	0.417	0.062	1.197	1.492	1,130	0.250
	7/24/58	1954	4_2	16.409	22	0.348	0.129				
Wood R.	7/11/56	1952	4_2	16.339	118	0.346	0.054	1.225	0.090	1,238	0.789
	7/5/58	1954	4_2	16.361	122	0.282	0.048				
”	7/11/56	1951	5_2	16.435	46	0.296	0.081	0.304[a]	0.552	2,112	0.587
	7/17/57	1952	5_2	16.467	45	0.346	0.089				
	7/5/58	1953	5_2	16.583	24	0.341	0.122				
Naknek R.	7/6/56	1951	5_2	16.214	28	0.323	0.109	3.984[a]	0.830	3,203	0.318
	7/8/56	1951	5_2	16.206	34	0.350	0.103				
	7/3, 5, 11, 12, 25/57	1952	5_2	16.324	127	0.316	0.050				
	7/9/58	1953	5_2	16.167	18	0.147	0.093				
”	7/6/56	1951	5_3	16.118	17	0.110	0.026	3.064[b]	1.874	1,84	0.175
	7/9, 13, 19/58	1953	5_3	16.319	69	0.338	0.071				
”	7/6/56	1950	6_3	16.210	38	0.278	0.015	16.000[a,c]	1.013	3,415	0.399
	7/8/56	1950	6_3	16.316	38	0.816	0.149				
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	16.268	325	0.363	0.033				
	7/9/58	1952	6_3	16.500	18	0.500	0.171				

$$C = -2 \sum \ln P_i = 46.471$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5g. Effect of year class on number of anal fin rays in sockeye salmon collected in 1955–58.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	18.150	60	0.435	0.086	1.060	0.044	1,145	0.835
	7/1, 31/58	1953	5_2	18.126	87	0.461	0.073				
„	7/25, 27, 28/57	1951	6_3	18.133	75	0.387	0.072	1.049	10.373[c]	1,158	0.001
	7/1, 31/58	1952	6_3	18.447	85	0.369	0.066				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	17.800	15	0.314	0.150	0.045[a]	1.643	2,99	0.226
	6/20/57	1952	5_3	18.062	32	0.318	0.101				
	6/26/58	1953	5_3	18.091	53	0.306	0.077				
„	9/7/56	1951	5_3	18.062	16	0.329	0.148	0.769[a]	6.464[c]	2,101	0.003
	8/21, 9/9, 17/57	1952	5_3	17.941	68	0.355	0.073				
	8/31/58	1953	5_3	18.500	20	0.474	0.158				
„	6/16, 29/55	1949	6_4	17.947	38	0.322	0.093	0.325[a]	0.048	2,133	0.950
	6/22/56	1950	6_4	17.909	55	0.380	0.084				
	6/26/58	1952	6_4	17.930	43	0.352	0.092				
„	8/24/55	1949	6_4	17.944	18	0.173	0.101	8.869[a,b]	5.103[c]	3,169	0.003
	9/7/56	1950	6_4	18.014	69	0.250	0.061				
	8/21, 9/9, 17/57	1951	6_4	17.931	58	0.416	0.085				
	8/31/58	1952	6_4	18.429	28	0.476	0.133				
Red R.	6/18/56	1951	5_3	18.214	28	0.471	0.132	1.794[a]	0.941	2,122	0.407
	6/21/57	1952	5_3	18.386	57	0.348	0.079				
	6/24/58	1953	5_3	18.425	40	0.507	0.114				
Bristol Bay											
Egegik R.	7/17/56	1951	5_3	17.909	110	0.377	0.059	4.455[a]	9.240[c]	2,220	0.001
	7/13/57	1952	5_3	18.625	16	0.783	0.229				
	7/7/58	1953	5_3	18.144	97	0.479	0.071				
„	7/17/56	1950	6_3	18.000	16	0.667	0.211	3.210[a]	1.589	2,171	0.232
	7/13/57	1951	6_3	18.019	105	0.365	0.059				
	7/7/58	1952	6_3	18.208	53	0.475	0.096				
Ugashik R.	7/19/57	1952	5_2	18.030	66	0.368	0.075	1.136	1.241	1,114	0.265
	7/16/58	1953	5_2	17.900	50	0.418	0.092				
„	7/23/56	1951	5_3	17.853	34	0.311	0.097	0.089[a]	2.320	2,134	0.107
	7/19/57	1952	5_3	17.933	30	0.340	0.108				
	7/16/58	1953	5_3	18.096	73	0.338	0.068				
Kvichak R.	7/13/56	1951	5_3	17.939	49	0.350	0.085	2.439[a]	4.118[b]	2,252	0.019
	7/10/57	1952	5_3	18.148	27	0.516	0.141				
	7/10, 16, 24/58	1953	5_3	18.257	179	0.507	0.053				
„	7/13/56	1952	4_2	17.862	109	0.435	0.063	1.146	0.378	1,130	0.540
	7/24/58	1954	4_2	17.956	23	0.498	0.150				
Wood R.	7/11/56	1952	4_2	18.008	117	0.474	0.064	1.273	3.460	1,236	0.070
	7/5/58	1954	4_2	18.165	121	0.372	0.130				
„	7/11/56	1951	5_2	18.000	46	0.489	0.104	0.999[a]	0.300	2,112	0.746
	7/17/57	1952	5_2	18.044	45	0.362	0.091				
	7/5/58	1953	5_2	17.917	24	0.428	0.136				

Continued . . .

Appendix Table 5g. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Naknek R.	7/6/56	1951	5_2	17.963	27	0.499	0.138	6.349[a]	0.570	3,200	0.641
	7/8/56	1951	5_2	18.000	34	0.242	0.086				
	7/3, 5, 11, 12, 25/57	1952	5_2	17.960	126	0.422	0.058				
	7/9/58	1953	5_2	18.176	17	0.654	0.202				
"	7/6/56	1951	5_3	17.941	17	0.434	0.165	1.080	3.419	1,84	0.065
	7/9, 13, 19/58	1953	5_3	18.261	69	0.402	0.077				
"	7/6/56	1950	6_3	17.816	38	0.316	0.092	4.797[a]	7.582[c]	3,414	0.001
	7/8/56	1950	6_3	17.949	39	0.524	0.117				
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	18.034	324	0.497	0.039				
	7/9/58	1952	6_3	18.765	17	0.691	0.208				

$$C = -2 \sum \ln P_i = 101.387^{c}$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5h. Effect of year class on number of scales along the lateral line in sockeye salmon collected in 1956–59.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	131.317	60	4.457	0.275	2.865[a]	0.372	2,162	0.491
	7/1, 31/58	1953	5_2	131.046	88	2.986	0.185				
	6/29/59	1954	5_2	131.118	17	3.362	0.445				
"	7/31/58	1953	5_3	131.158	19	1.807	0.308	1.667	0.000	1,41	0.999
	8/2/59	1954	5_3	131.167	24	3.013	0.355				
"	7/25, 27, 28/57	1951	6_3	130.986	74	3.055	0.205	6.439[a,b]	0.082	2,276	0.928
	7/1, 31/58	1952	6_3	130.882	85	2.486	0.172				
	6/29, 8/2/59	1953	6_3	130.975	120	4.378	0.190				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	130.000	15	5.429	0.623	3.883[a]	0.529	3,133	0.533
	6/20/57	1952	5_3	129.576	33	2.314	0.269				
	6/26/58	1953	5_3	130.073	55	3.441	0.252				
	6/24/59	1954	5_3	129.882	34	3.197	0.306				
"	6/22/56	1950	6_4	129.891	55	3.136	0.239	2.610[a]	0.111	2,131	0.705
	6/26/58	1952	6_4	130.070	43	4.924	0.338				
	6/24/59	1953	6_4	129.917	36	3.449	0.310				

Continued . . .

Appendix Table 5h. Continued.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Red R.	6/18/56	1951	5_3	131.290	31	3.280	0.331	4.394[a]	5.369	3,143	0.002
	6/21/57	1952	5_3	130.672	58	2.821	0.222				
	6/24/58	1953	5_3	131.512	41	1.706	0.207				
	6/25/59	1954	5_3	132.294	17	2.094	0.351				
Bristol Bay											
Naknek R.	7/6/56	1951	5_3	131.471	17	6.890	0.656	8.726[a,b]	3.632	2,225	0.046
	7/9, 13, 19/58	1953	5_3	130.333	69	5.343	0.280				
	7/2/59	1954	5_3	130.077	142	3.235	0.152				
Egegik R.	7/17/56	1951	5_3	130.009	110	2.468	0.150	5.920[a]	1.504	3,317	0.239
	7/13/57	1952	5_3	129.375	16	4.917	0.573				
	7/7/58	1953	5_3	130.192	99	3.565	0.191				
	7/7/59	1954	5_3	130.292	96	2.756	0.170				
"	7/17/56	1950	6_3	130.250	16	4.600	0.554	5.806[a]	0.301	3,215	0.775
	7/13/57	1951	6_3	130.377	106	4.294	0.202				
	7/7/58	1952	6_3	130.130	54	2.794	0.230				
	7/7/59	1953	6_3	130.116	43	2.581	0.245				
Ugashik R.	7/23/56	1951	5_3	129.743	35	3.844	0.336	1.552[a]	3.982[c]	3,217	0.021
	7/19/57	1952	5_3	129.900	30	2.783	0.310				
	7/16/58	1953	5_3	130.726	73	2.757	0.196				
	7/11/59	1954	5_3	130.651	83	2.840	0.184				
Kvichak R.	7/13/56	1952	4_2	130.815	108	4.377	0.202	0.721[a]	0.075	2,161	0.922
	7/24/58	1954	4_2	130.913	23	4.174	0.436				
	7/9/59	1955	4_2	130.970	33	5.468	0.407				
"	7/13/56	1951	5_3	131.528	53	3.941	0.275	20.722[a,c]	6.967[c]	3,605	0.001
	7/10/57	1952	5_3	131.655	29	3.734	0.365				
	7/10, 16, 24/58	1953	5_3	131.760	179	6.411	0.189				
	7/9, 14, 26/59	1954	5_3	130.914	348	3.635	0.100				
Wood R.	7/11/56	1952	4_2	129.864	118	3.520	0.173	1.104[a]	3.969[b]	2,357	0.009
	7/5/58	1954	4_2	130.410	122	3.302	0.165				
	6/29/59	1955	4_2	129.775	120	3.991	0.182				
"	7/11/56	1951	5_2	130.500	46	2.656	0.243	2.007[a]	2.532	3,126	0.064
	7/17/57	1952	5_2	129.556	45	3.389	0.278				
	7/5/58	1953	5_2	130.375	24	2.332	0.318				
	6/29/59	1954	5_2	130.267	15	4.064	0.164				

$$C = -2 \sum \ln P_i = 62.115^{c}$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5i. Effect of year class on number of vertebrae in sockeye salmon collected in 1956–59.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values: Variance ratio	F-values: Analysis of variance	d. f.	P
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	67.508	59	0.875	0.123	4.754[a]	2.126	2,159	0.138
	7/1, 31/58	1953	5_2	67.218	87	0.684	0.089				
	6/29/59	1954	5_2	67.250	16	0.333	0.145				
”	7/31/58	1953	5_3	67.526	19	0.930	0.221	1.158	0.015	1,40	0.900
	8/2/59	1954	5_3	67.565	23	1.077	0.217				
”	7/25, 27, 28/57	1951	6_3	67.197	71	0.589	0.092	3.764[a]	0.545	2,271	0.609
	7/1, 31/58	1952	6_3	67.306	85	0.715	0.092				
	6/29, 8/2/59	1953	6_3	67.331	118	0.890	0.089				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	66.800	15	0.743	0.230	2.588[a]	0.367	3,132	0.822
	6/20/57	1952	5_3	67.030	33	0.592	0.136				
	6/26/58	1953	5_3	66.944	54	0.544	0.101				
	6/24/59	1954	5_3	66.912	34	0.385	0.105				
”	6/22/56	1950	6_4	66.891	55	0.654	0.110	0.463[a]	0.660	2,130	0.677
	6/26/58	1952	6_4	67.023	43	0.642	0.124				
	6/24/59	1953	6_4	67.086	35	0.785	0.148				
Red R.	6/18/56	1951	5_3	67.677	31	0.492	0.128	0.551[a]	3.224[b]	3,139	0.025
	6/21/57	1952	5_3	67.393	56	0.606	0.104				
	6/24/58	1953	5_3	67.590	39	0.406	0.102				
	6/25/59	1954	5_3	68.000	17	0.750	0.210				
Bristol Bay											
Naknek R.	7/6/56	1951	5_3	67.588	17	1.132	0.266	12.580[a,c]	3.069[b]	2,222	0.024
	7/9, 13, 19/58	1953	5_3	67.319	69	1.220	0.134				
	7/2/59	1954	5_3	67.094	139	0.607	0.063				
Egegik R.	7/17/56	1951	5_3	67.234	111	0.526	0.069	2.402[a]	0.249	3,316	0.739
	7/13/57	1952	5_3	67.125	16	0.650	0.208				
	7/7/58	1953	5_3	67.165	97	0.556	0.076				
	7/7/59	1954	5_3	67.156	96	0.702	0.084				
”	7/17/56	1950	6_3	67.188	16	0.829	0.235	1.859[a]	2.026	3,213	0.118
	7/13/57	1951	6_3	67.371	105	0.736	0.084				
	7/7/58	1952	6_3	67.132	53	0.578	0.105				
	7/7/59	1953	6_3	67.047	43	0.569	0.114				
Ugashik R.	7/23/56	1951	5_3	67.265	34	0.625	0.138	1.774[a]	3.302[b]	3,213	0.023
	7/19/57	1952	5_3	67.233	30	0.530	0.135				
	7/16/58	1953	5_3	67.444	72	0.645	0.095				
	7/11/59	1954	5_3	67.062	81	0.484	0.077				
Kvichak R.	7/13/56	1952	4_2	67.373	110	0.676	0.077	5.512[a]	0.483	2,163	0.625
	7/24/58	1954	4_2	67.565	23	0.621	0.168				
	7/9/59	1955	4_2	67.364	33	1.239	0.195				
”	7/13/56	1951	5_3	67.608	51	0.923	0.136	8.466[a,b]	9.255[c]	3,592	0.001
	7/10/57	1952	5_3	67.793	29	1.098	0.195				
	7/10, 16, 24/58	1953	5_3	67.874	174	1.128	0.105				
	7/9, 14, 26/59	1954	5_3	67.418	342	0.784	0.045				

Continued . . .

Appendix Table 5i. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
	7/11/56	1952	4_2	67.254	118	0.602	0.072				
Wood R.	7/5/58	1954	4_2	67.250	120	0.626	0.073	9.583[a,c]	0.796	2,357	0.461
	6/29/59	1955	4_2	67.131	122	0.991	0.089				
	7/11/56	1951	5_2	67.422	45	0.840	0.138				
	7/17/57	1952	5_2	67.091	44	0.550	0.113				
”	7/5/58	1953	5_2	67.130	23	0.573	0.161	2.694[a]	1.403	3,122	0.264
	6/29/59	1954	5_2	67.214	14	0.492	0.063				

$$C = -2 \sum \ln P_i = 52.565^{c}$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5j. Effect of year class on position of the first haemal arch in sockeye salmon collected in 1956–59.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
	7/26, 27, 28/57	1952	5_2	34.814	59	0.534	0.096				
Chignik R.	7/1, 31/58	1953	5_2	34.563	87	0.668	0.088	3.374[a]	2.098	2,160	0.141
	6/29/59	1954	5_2	34.529	17	0.388	0.152				
”	7/31/58	1953	5_3	34.789	19	0.620	0.182	1.082	0.112	1,40	0.735
	8/2/59	1954	5_3	34.870	23	0.573	0.158				
	7/25, 27, 28/57	1951	6_3	34.417	72	1.007	0.119				
”	7/1, 31/58	1952	6_3	34.612	85	0.716	0.092	5.108	0.983	2,272	0.388
	6/29, 8/2/59	1953	6_3	34.542	117	0.660	0.074				
Kodiak Island											
	6/22/56	1951	5_3	34.567	15	0.552	0.199				
	6/20/57	1952	5_3	34.515	33	0.508	0.126				
Karluk R.	6/26/58	1953	5_3	34.309	55	0.736	0.117	2.399[a]	0.534	3,134	0.465
	6/24/59	1954	5_3	34.400	35	0.482	0.118				
	6/22/56	1950	6_4	34.564	55	0.510	0.097				
”	6/26/58	1952	6_4	34.674	43	0.796	0.138	8.645[a,c]	0.297	2,131	0.748
	6/24/59	1953	6_4	34.694	36	1.246	0.187				
	6/18/56	1951	5_3	34.806	31	0.828	0.166				
	6/21/57	1952	5_3	34.536	56	0.617	0.106				
Red R.	6/24/58	1953	5_3	34.658	41	0.530	0.115	2.840[a]	1.405	3,141	0.264
	6/25/59	1954	5_3	34.941	17	0.931	0.234				
Bristol Bay											
	7/6/56	1951	5_3	34.588	17	0.882	0.228				
Naknek R.	7/9, 13, 19/58	1953	5_3	34.643	70	0.986	0.119	3.695	0.762	2,224	0.475
	7/2/59	1954	5_3	34.486	140	0.669	0.069				

Continued . . .

APPENDIX TABLE 5j. Continued.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Egegik R.	7/17/56	1951	5_3	34.568	111	0.466	0.065	10.013[a,c]	0.266	3,316	0.850
	7/13/57	1952	5_3	34.500	16	0.533	0.189				
	7/7/58	1953	5_3	34.639	97	0.754	0.089				
	7/7/59	1954	5_3	34.552	96	0.839	0.092				
”	7/17/56	1950	6_3	34.375	16	1.317	0.296	10.199[a,c]	0.201	3,216	0.895
	7/13/57	1951	6_3	34.481	106	0.614	0.076				
	7/7/58	1952	6_3	34.389	54	0.620	0.108				
	7/7/59	1953	6_3	34.432	43	0.530	0.110				
Ugashik R.	7/23/56	1951	5_3	34.382	34	0.668	0.142	1.627[a]	1.649	3,215	0.205
	7/19/57	1952	5_3	34.800	30	0.786	0.165				
	7/16/58	1953	5_3	34.625	72	0.604	0.116				
	7/11/59	1954	5_3	34.542	83	0.544	0.081				
Kvichak R.	7/13/56	1952	4_2	34.712	111	0.807	0.086	4.481[a]	2.498	2,164	0.088
	7/24/58	1954	4_2	34.826	23	0.696	0.178				
	7/9/59	1955	4_2	34.364	33	0.676	0.141				
”	7/13/56	1951	5_3	34.863	51	0.681	0.136	12.990[a,c]	3.111[b]	3,599	0.026
	7/10/57	1952	5_3	34.897	29	0.882	0.177				
	7/10, 16, 24/58	1953	5_3	34.922	178	0.875	0.070				
	7/9, 14, 26/59	1954	5_3	34.690	345	0.703	0.045				
Wood R.	7/11/56	1952	4_2	34.339	118	0.619	0.073	1.241[a]	0.842	2,357	0.443
	7/5/58	1954	4_2	34.217	120	0.675	0.075				
	6/29/59	1955	4_2	34.320	122	0.550	0.067				
”	7/11/56	1951	5_2	34.456	46	0.787	0.132	3.777[a]	0.409	3,124	0.748
	7/17/57	1952	5_2	34·409	44	0.433	0.099				
	7/5/58	1953	5_2	34.391	23	0.613	0.167				
	6/29/59	1954	5_2	34.200	15	0.600	0.063				

$$C = -2 \sum \ln P_i = 30.779$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

APPENDIX TABLE 5k. Effect of year class on number of ventral gill rakers in sockeye salmon collected in 1956–59.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance eatio	Analysis of variance	d. f.	*P*
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	23.400	60	0.685	0.108	0.076[a]	5.591[c]	2,161	0.003
	7/1, 31/58	1953	5_2	23.207	87	0.678	0.089				
	6/29/59	1954	5_2	22.647	17	0.619	0.190				
”	7/31/58	1953	5_3	23.105	19	1.099	0.241	1.147	0.323	1,42	0.570
	8/2/59	1954	5_3	23.280	25	0.958	0.195				

Continued . . .

Appendix Table 5k. Continued.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Chignik R.	7/25, 27, 28/57	1951	6_3	23.227	75	0.772	0.102	3.726[a]	0.048	2,276	0.953
	7/1, 31/58	1952	6_3	23.259	85	0.742	0.094				
	6/29, 8/2/59	1953	6_3	23.218	119	1.054	0.095				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	22.533	15	0.552	0.199	2.308[a]	1.439	3,134	0.256
	6/20/57	1952	5_3	22.485	33	1.133	0.188				
	6/26/58	1953	5_3	22.527	55	0.958	0.133				
	6/24/59	1954	5_3	22.114	35	1.044	0.173				
"	6/22/56	1950	6_4	22.364	55	0.569	0.103	2.820[a]	0.544	2,131	0.591
	6/26/58	1952	6_4	22.419	43	0.868	0.144				
	6/24/59	1953	6_4	22.556	36	0.883	0.155				
Red R.	6/18/56	1951	5_3	22.871	31	1.050	0.184	4.889[a]	0.742	3,143	0.532
	6/21/57	1952	5_3	22.914	58	0.922	0.127				
	6/24/58	1953	5_3	22.707	41	0.562	0.119				
	6/25/59	1954	5_3	23.059	17	0.556	0.182				
Bristol Bay											
Naknek R.	7/6/56	1951	5_3	23.125	16	0.517	0.186	3.043[a]	2.271	2,225	0.111
	7/9, 13, 19/58	1953	5_3	22.714	70	0.758	0.105				
	7/2/59	1954	5_3	22.972	142	0.964	0.084				
Egegik R.	7/17/56	1951	5_3	23.045	110	0.888	0.090	0.288[a]	1.309	3,319	0.282
	7/13/57	1952	5_3	23.000	16	0.933	0.249				
	7/7/58	1953	5_3	22.980	99	0.918	0.096				
	7/7/59	1954	5_3	22.796	98	0.824	0.089				
"	7/17/56	1950	6_3	22.938	16	0.996	0.258	0.534[a]	3.537[b]	3,216	0.017
	7/13/57	1951	6_3	22.962	106	0.894	0.092				
	7/7/58	1952	6_3	22.630	54	1.068	0.142				
	7/7/59	1953	6_3	23.273	44	0.947	0.148				
Ugashik R.	7/23/56	1951	5_3	22.765	34	0.670	0.143	4.476[a]	1.431	3,216	0.255
	7/19/57	1952	5_3	23.000	30	1.310	0.213				
	7/16/58	1953	5_3	23.082	73	0.854	0.109				
	7/11/59	1954	5_3	23.145	83	0.759	0.095				
Kvichak R.	7/13/56	1952	4_2	23.100	110	0.770	0.084	1.155[a]	1.543	2,163	0.241
	7/24/58	1954	4_2	22.739	23	1.020	0.215				
	7/9/59	1955	4_2	22.970	33	0.968	0.170				
"	7/13/56	1951	5_3	23.058	52	0.840	0.128	0.624[a]	2.576	3,605	0.054
	7/10/57	1952	5_3	23.379	29	0.815	0.171				
	7/10, 16, 24/58	1953	5_3	22.972	179	0.904	0.071				
	7/9, 14, 26/59	1954	5_3	22.894	349	0.951	0.055				
Wood R.	7/11/56	1952	4_2	22.636	118	0.746	0.080	2.682[a]	4.884[c]	2,360	0.009
	7/5/58	1954	4_2	22.967	122	0.991	0.090				
	6/29/59	1955	4_2	22.967	123	0.950	0.089				
"	7/11/56	1951	5_2	23.089	45	1.219	0.166	6.039[a,c]	1.658	3,126	0.207
	7/17/57	1952	5_2	22.667	45	0.682	0.124				
	7/5/58	1953	5_2	22.833	24	0.667	0.170				
	6/29/59	1954	5_2	23.063	16	1.127	0.084				

$C = -2 \sum \ln P_i = 56.943$[c]

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[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 51. Effect of year class on total number of gill rakers in sockeye salmon collected in 1956–59.

Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	*F*-values		d. f.	*P*
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	37.667	60	1.751	0.172	0.634[a]	4.898[c]	2,161	0.009
	7/1, 31/58	1953	5_2	37.506	87	1.462	0.130				
	6/29/59	1954	5_2	36.588	17	1.756	0.321				
"	7/31/58	1953	5_3	37.526	19	2.263	0.345	1.165	0.649	1,42	0.436
	8/2/59	1954	5_3	37.880	25	1.942	0.279				
"	7/25, 27, 28/57	1951	6_3	37.400	75	1.730	0.153	4.623[a]	0.282	2,276	0.760
	7/1, 31/58	1952	6_3	37.471	85	1.324	0.126				
	6/29, 8/2/59	1953	6_3	37.546	119	2.148	0.134				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	36.533	15	2.114	0.389	1.169[a]	1.384	3,134	0.269
	6/20/57	1952	5_3	36.364	33	2.676	0.289				
	6/26/58	1953	5_3	36.418	55	1.914	0.188				
	6/24/59	1954	5_3	35.857	35	2.185	0.248				
"	6/22/56	1950	6_4	36.189	53	1.387	0.163	2.517[a]	0.646	2,129	0.531
	6/26/58	1952	6_4	36.442	43	1.824	0.208				
	6/24/59	1953	6_4	36.472	36	2.257	0.251				
Red R.	6/18/56	1951	5_3	36.806	31	1.761	0.242	0.501[a]	0.642	3,143	0.596
	6/21/57	1952	5_3	37.086	58	1.974	0.186				
	6/24/58	1953	5_3	36.902	41	1.640	0.202				
	6/25/59	1954	5_3	37.294	17	1.594	0.306				
Bristol Bay											
Naknek R.	7/6/56	1951	5_3	37.125	16	1.183	0.281	1.484[a]	3.591[b]	2,225	0.031
	7/9, 13, 19/58	1953	5_3	36.471	70	1.992	0.170				
	7/2/59	1954	5_3	36.972	142	1.843	0.114				
Egegik R.	7/17/56	1951	5_3	37.300	110	1.955	0.134	0.515[a]	0.149	3,319	0.929
	7/13/57	1952	5_3	37.188	16	2.020	0.368				
	7/7/58	1953	5_3	37.182	99	1.701	0.132				
	7/7/59	1954	5_3	37.265	98	1.805	0.134				
"	7/17/56	1950	6_3	37.250	16	1.400	0.305	1.366[a]	2.301	3,216	0.082
	7/13/57	1951	6_3	37.189	106	1.719	0.128				
	7/7/58	1952	6_3	37.019	54	2.018	0.195				
	7/7/59	1953	6_3	37.705	44	1.794	0.202				
Ugashik R.	7/23/56	1951	5_3	36.765	34	1.700	0.227	6.321[a]	4.152[b]	3,216	0.008
	7/19/57	1952	5_3	37.000	30	3.034	0.323				
	7/16/58	1953	5_3	37.288	73	1.791	0.158				
	7/11/59	1954	5_3	37.675	83	1.759	0.145				
Kvichak R.	7/13/56	1952	4_2	37.391	110	1.396	0.113	2.925[a]	2.471	2,163	0.090
	7/24/58	1954	4_2	36.826	23	2.332	0.326				
	7/9/59	1955	4_2	37.030	33	1.780	0.232				
"	7/13/56	1951	5_3	37.346	52	1.956	0.196	0.117[a]	2.284	3,605	0.083
	7/10/57	1952	5_3	37.793	29	2.026	0.269				
	7/10, 16, 24/58	1953	5_3	37.112	179	2.077	0.108				
	7/9, 14, 26/59	1954	5_3	37.115	349	2.199	0.077				

Continued . . .

Appendix Table 5l. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Wood R.	7/11/56	1952	4_2	36.500	118	1.842	0.125	0.089[a]	9.577[c]	2,360	0.001
	7/5/58	1954	4_2	37.156	122	1.901	0.125				
	6/29/59	1955	4_2	37.195	123	1.962	0.126				
"	7/11/56	1951	5_2	37.200	45	2.573	0.242	6.322[a,b]	1.898	3,126	0.153
	7/17/57	1952	5_2	36.578	45	1.431	0.180				
	7/5/58	1953	5_2	37.000	24	1.304	0.238				
	6/29/59	1954	5_2	37.313	16	2.760	0.130				

$C = -2 \sum \ln P_i = 65.675$[c]

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5m. Effect of year class on number of pectoral fin rays in sockeye salmon collected in 1956–59.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	16.350	60	0.367	0.091	6.496[a,b]	1.987	2,161	0.162
	7/1, 31/58	1953	5_2	16.184	87	0.222	0.050				
	6/29/59	1954	5_2	16.176	17	0.156	0.095				
"	7/31/58	1953	5_3	16.421	19	0.480	0.158	1.745	0.978	1,42	0.328
	8/2/59	1954	5_3	16.240	25	0.275	0.105				
"	7/25, 27, 28/57	1951	6_3	16.333	75	0.279	0.061	3.574[a]	1.302	2,277	0.139
	7/1, 31/58	1952	6_3	16.400	85	0.243	0.054				
	6/29, 8/2/59	1953	6_3	16.275	120	0.352	0.055				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	16.533	15	0.267	0.138	1.540[a]	2.499	3,133	0.066
	6/20/57	1952	5_3	16.636	33	0.301	0.097				
	6/26/58	1953	5_3	16.315	54	0.258	0.070				
	6/24/59	1954	5_3	16.457	35	0.374	0.105				
"	6/22/56	1950	6_4	16.491	55	0.329	0.078	3.030[a]	0.544	2,131	0.591
	6/26/58	1952	6_4	16.372	43	0.239	0.075				
	6/24/59	1953	6_4	16.417	36	0.420	0.110				
Red R.	6/18/56	1951	5_3	16.581	31	0.318	0.103	0.266[a]	0.035	3,143	0.991
	6/21/57	1952	5_3	16.551	58	0.322	0.075				
	6/24/58	1953	5_3	16.561	41	0.302	0.087				
	6/25/59	1954	5_3	16.529	17	0.262	0.122				
Bristol Bay											
Naknek R.	7/6/56	1951	5_3	16.118	17	0.110	0.026	6.344[a,b]	1.588	2,223	0.232
	7/9, 13, 19/58	1953	5_3	16.319	69	0.338	0.071				
	7/2/59	1954	5_3	16.193	140	0.301	0.047				

Continued . . .

Appendix Table 5m. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Egegik R.	7/17/56	1951	5_3	16.486	111	0.307	0.053	0.152[a]	1.084	3,320	0.368
	7/13/57	1952	5_3	16.750	16	0.333	0.149				
	7/7/58	1953	5_3	16.505	99	0.314	0.057				
	7/7/59	1954	5_3	16.541	98	0.333	0.058				
”	7/17/56	1950	6_3	16.500	16	0.267	0.133	1.315[a]	1.818	3,215	0.166
	7/13/57	1951	6_3	16.396	106	0.270	0.050				
	7/7/58	1952	6_3	16.556	54	0.252	0.069				
	7/7/59	1953	6_3	16.581	43	0.344	0.089				
Ugashik R.	7/23/56	1951	5_3	16.471	34	0.257	0.088	2.694[a]	0.700	3,216	0.559
	7/19/57	1952	5_3	16.300	30	0.424	0.121				
	7/16/58	1953	5_3	16.452	73	0.279	0.062				
	7/11/59	1954	5_3	16.386	83	0.337	0.063				
Kvichak R.	7/13/56	1952	4_2	16.518	110	0.417	0.062	0.636[a]	1.579	2,162	0.235
	7/24/58	1954	4_2	16.409	22	0.348	0.129				
	7/9/59	1955	4_2	16.303	33	0.343	0.100				
”	7/13/56	1951	5_3	16.365	52	0.315	0.079	0.568[a]	1.288	3,606	0.286
	7/10/57	1952	5_3	16.552	29	0.328	0.108				
	7/10, 16, 24/58	1953	5_3	16.330	179	0.335	0.043				
	7/9, 14, 26/59	1954	5_3	16.334	350	0.361	0.032				
Wood R.	7/11/56	1952	4_2	16.339	118	0.346	0.054	1.205[a]	0.860	2,359	0.436
	7/5/58	1954	4_2	16.361	122	0.282	0.048				
	6/29/59	1955	4_2	16.270	122	0.315	0.051				
”	7/11/56	1951	5_2	16.435	46	0.296	0.081	0.600[a]	0.365	3,127	0.779
	7/17/57	1952	5_2	16.467	45	0.346	0.089				
	7/5/58	1953	5_2	16.583	24	0.341	0.122				
	6/29/59	1954	5_2	16.500	16	0.400	0.045				

$$C = -2 \sum \ln P_i = 33.558$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

Appendix Table 5n. Effect of year class on number of anal fin rays in sockeye salmon collected in 1956–59.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Alaska Peninsula											
Chignik R.	7/26, 27, 28/57	1952	5_2	18.150	60	0.435	0.086	0.316[a]	0.834	2,161	0.447
	7/1, 31/58	1953	5_2	18.126	87	0.461	0.073				
	6/29/59	1954	5_2	18.353	17	0.369	0.148				
”	7/31/58	1953	5_3	18.421	19	0.591	0.176	2.442[b]	3.202	3,202	0.080
	8/2/59	1954	5_3	18.080	25	0.242	0.100				

Continued . . .

Appendix Table 5n. Continued.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Chignik R.	7/25, 27, 28/57	1951	6_3	18.133	75	0.387	0.072	2.824[a]	8.059[c]	2,276	0.001
	7/1, 31/58	1952	6_3	18.447	85	0.369	0.066				
	6/29, 8/2/59	1953	6_3	18.151	119	0.282	0.045				
Kodiak Island											
Karluk R.	6/22/56	1951	5_3	17.800	15	0.314	0.148	3.710[a]	1.151	3,133	0.340
	6/20/57	1952	5_3	18.062	32	0.318	0.073				
	6/26/58	1953	5_3	18.091	53	0.306	0.158				
	6/24/59	1954	5_3	17.943	35	0.526	0.122				
"	6/22/56	1950	6_4	17.909	55	0.380	0.084	1.718[a]	1.577	2,131	0.236
	6/26/58	1952	6_4	17.930	43	0.352	0.092				
	6/24/59	1953	6_4	18.139	36	0.523	0.118				
Red R.	6/18/56	1951	5_3	18.214	28	0.471	0.132	1.962[a]	0.617	3,138	0.611
	6/21/57	1952	5_3	18.386	57	0.348	0.079				
	6/24/58	1953	5_3	18.425	40	0.507	0.114				
	6/25/59	1954	5_3	18.353	17	0.494	0.170				
Bristol Bay											
Naknek R.	7/6/56	1951	5_3	17.941	17	0.434	0.165	0.062[a]	2.102	2,224	0.141
	7/9, 13, 19/58	1953	5_3	18.261	69	0.402	0.077				
	7/2/59	1954	5_3	18.121	141	0.407	0.054				
Egegik R.	7/17/56	1951	5_3	17.909	110	0.377	0.059	4.536[a]	6.216[c]	3,316	0.001
	7/13/57	1952	5_3	18.625	16	0.783	0.229				
	7/7/58	1953	5_3	18.144	97	0.479	0.071				
	7/7/59	1954	5_3	18.010	97	0.469	0.070				
"	7/17/56	1950	6_3	18.000	16	0.667	0.211	3.523[a]	1.111	3,214	0.354
	7/13/57	1951	6_3	18.019	105	0.365	0.059				
	7/7/58	1952	6_3	18.208	53	0.475	0.096				
	7/7/59	1953	6_3	18.045	44	0.370	0.091				
Ugashik R.	7/23/56	1951	5_3	17.853	34	0.311	0.097	0.503[a]	1.652	3,216	0.205
	7/19/57	1952	5_3	17.933	30	0.340	0.108				
	7/16/58	1953	5_3	18.096	73	0.338	0.068				
	7/11/59	1954	5_3	18.024	83	0.292	0.059				
Kvichak R.	7/13/56	1952	4_2	17.862	109	0.435	0.063	0.344[a]	1.556	2,162	0.238
	7/24/58	1954	4_2	17.956	23	0.498	0.150				
	7/9/59	1955	4_2	18.091	33	0.398	0.110				
"	7/13/56	1951	5_3	17.939	49	0.350	0.085	3.302[a]	5.266[c]	3,598	0.001
	7/10/57	1952	5_3	18.148	27	0.516	0.141				
	7/10, 16, 24/58	1953	5_3	18.257	179	0.507	0.053				
	7/9, 14, 26/59	1954	5_3	18.037	347	0.429	0.033				
Wood R.	7/11/56	1952	4_2	18.008	117	0.474	0.064	4.646[a]	4.010[b]	2,357	0.021
	7/5/58	1954	4_2	18.165	121	0.372	0.130				
	6/29/59	1955	4_2	18.246	122	0.451	0.060				
"	7/11/56	1951	5_2	18.000	46	0.489	0.104	1.026[a]	0.610	3,126	0.616
	7/17/57	1952	5_2	18.044	45	0.362	0.091				
	7/5/58	1953	5_2	17.917	24	0.428	0.136				
	6/29/59	1954	5_2	18.200	15	0.457	0.055				

$C = -2 \sum \ln P_i = 74.870$[b]

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5o. Effect of year class on number of scales along the lateral line in sockeye salmon collected in 1956–60.

								F-values			
Area	Date	Year class	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/13/56	1952	4_2	130.815	108	4.377	0.202	2.461[a]	2.191	3,453	0.092
	7/24/58	1954	4_2	130.913	23	4.174	0.436				
	7/9/59	1955	4_2	130.970	33	5.468	0.407				
	7/2, 8, 21/60	1956	4_2	131.358	293	3.813	0.114				
Wood R.	7/11/56	1952	4_2	129.864	118	3.520	0.173	0.135[a]	3.440[b]	3,431	0.036
	7/5/58	1954	4_2	130.410	122	3.302	0.165				
	6/29/59	1955	4_2	129.775	120	3.991	0.182				
	7/7/60	1956	4_2	130.387	75	3.484	0.214				
„	7/11/56	1951	5_2	130.500	46	2.656	0.243	2.711[a]	2.165	4,174	0.078
	7/17/57	1952	5_2	129.556	45	3.389	0.278				
	7/5/58	1953	5_2	130.375	24	2.332	0.318				
	6/29/59	1954	5_2	130.267	15	4.064	0.520				
	7/7/60	1955	5_2	130.490	49	3.672	0.274				
Egegik R.	7/17/56	1952	4_2	129.655	29	2.164	0.274	1.159	4.941[b]	1,125	0.029
	7/11/60	1956	4_2	130.388	98	2.508	0.161				
„	7/17/56	1951	5_3	130.009	110	2.468	0.150	7.091[a]	1.237	4,360	0.295
	7/13/57	1952	5_3	129.375	16	4.917	0.573				
	7/7/58	1953	5_3	130.192	99	3.565	0.191				
	7/7/59	1954	5_3	130.292	96	2.756	0.170				
	7/11/60	1955	5_3	130.273	44	2.342	0.230				
„	7/17/56	1950	6_3	130.250	16	4.600	0.554	7.730[a]	0.309	4,229	0.739
	7/13/57	1951	6_3	130.377	106	4.294	0.202				
	7/7/58	1952	6_3	130.130	54	2.794	0.230				
	7/7/59	1953	6_3	130.116	43	2.581	0.245				
	7/11/60	1954	6_3	130.533	15	2.000	0.365				
Naknek R.	7/6/56	1951	5_3	131.471	17	6.890	0.656	24.066[a,c]	2.260	3,264	0.086
	7/9, 13, 19/58	1953	5_3	130.333	69	5.343	0.280				
	7/2/59	1954	5_3	130.077	142	3.235	0.152				
	7/7/60	1955	5_3	129.925	40	9.917	0.498				
„	7/6, 8/56	1950	6_3	130.064	77	5.618	0.270	3.073[a]	3.511[b]	3,436	0.017
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	130.901	324	4.665	0.120				
	7/9/58	1952	6_3	130.278	18	7.506	0.664				
	7/7/60	1954	6_3	130.238	21	4.290	0.452				
Ugashik R.	7/23/56	1952	4_2	130.933	123	4.065	0.368	1.623	1.738	2,317	0.205
	7/19/57	1953	4_2	130.244	30	2.940	0.155				
	7/14/60	1956	4_2	130.401	167	3.446	0.145				

$C = -2 \sum \ln P_i = 42.876$[c]

[a] Bartlett's test.
[b] Significant at 5-percent level.
[c] Significant at 1-percent level.

Appendix Table 5p. Effect of year class on number of vertebrae in sockeye salmon collected in 1956–60.

Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Bristol Bay											
Kvichak R.	7/13/56	1952	4_2	67.373	110	0.676	0.077	7.815[a]	0.519	3,451	0.671
	7/24/58	1954	4_2	67.565	23	0.621	0.168				
	7/9/59	1955	4_2	67.364	33	1.239	0.195				
	7/2, 8, 21/60	1956	4_2	67.457	289	0.686	0.045				
Wood R.	7/11/56	1952	4_2	67.254	118	0.602	0.072	12.515[a,b]	0.562	3,432	0.644
	7/5/58	1954	4_2	67.250	120	0.626	0.073				
	6/29/59	1955	4_2	67.131	122	0.991	0.089				
	7/7/60	1956	4_2	67.184	76	0.659	0.095				
″	7/11/56	1951	5_2	67.422	45	0.840	0.138	2.812[a]	1.226	4,168	0.300
	7/17/57	1952	5_2	67.091	44	0.550	0.113				
	7/5/58	1953	5_2	67.130	23	0.573	0.161				
	6/29/59	1954	5_2	67.214	14	0.492	0.187				
	7/7/60	1955	5_2	67.106	47	0.706	0.122				
Egegik R.	7/17/56	1952	4_2	67.172	29	0.504	0.130	1.088	0.006	1,120	0.999
	7/11/60	1956	4_2	67.161	93	0.463	0.071				
″	7/17/56	1951	5_3	67.234	111	0.526	0.069	2.381[a]	0.268	4,359	0.898
	7/13/57	1952	5_3	67.125	16	0.650	0.208				
	7/7/58	1953	5_3	67.165	97	0.556	0.076				
	7/7/59	1954	5_3	67.156	96	0.702	0.084				
	7/11/60	1955	5_3	67.114	44	0.615	0.118				
″	7/17/56	1950	6_3	67.188	16	0.829	0.235	3.436[a]	2.583[b]	4,226	0.041
	7/13/57	1951	6_3	67.371	105	0.736	0.084				
	7/7/58	1952	6_3	67.132	53	0.578	0.105				
	7/7/59	1953	6_3	67.047	43	0.569	0.114				
	7/11/60	1954	6_3	66.785	14	0.385	0.164				
Naknek R.	7/6/56	1951	5_3	67.588	17	1.132	0.266	7.881[a,b]	1.930	3,260	0.141
	7/9, 13, 19/58	1953	5_3	67.319	69	1.220	0.134				
	7/2/59	1954	5_3	67.094	139	0.607	0.063				
	7/7/60	1955	5_3	67.128	39	1.378	0.187				
″	7/6, 8/56	1950	6_3	67.394	76	1.253	0.126	2.827	3.802[b]	3,420	0.010
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	67.547	308	0.989	0.057				
	7/9/58	1952	6_3	67.278	18	1.271	0.273				
	7/7/60	1954	6_3	66.810	21	1.062	0.224				
Ugashik R.	7/23/56	1952	4_2	67.277	119	0.405	0.058	4.662	1.943	2,316	0.170
	7/19/57	1953	4_2	67.400	30	0.662	0.148				
	7/14/60	1956	4_2	67.159	170	0.560	0.055				

$$C = -2 \sum \ln P_i = 27.364$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5q. Effect of year class on position of the first haemal arch in sockeye salmon collected in 1956–60.

								F-values			
Area	Date	Year class	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/13/56	1952	4_2	34.712	111	0.807	0.086	1.516[a]	1.846	3,455	0.158
	7/24/58	1954	4_2	34.826	23	0.696	0.178				
	7/9/59	1955	4_2	34.364	33	0.676	0.141				
	7/2, 8, 21/60	1956	4_2	34.682	292	0.664	0.045				
Wood R.	7/11/56	1952	4_2	34.339	118	0.619	0.073	1.626[a]	1.030	3,434	0.391
	7/5/58	1954	4_2	34.217	120	0.675	0.075				
	6/29/59	1955	4_2	34.320	122	0.550	0.063				
	7/7/60	1956	4_2	34.410	78	0.687	0.095				
”	7/11/56	1951	5_2	34.456	46	0.787	0.132	3.965[a]	0.505	4,171	0.731
	7/17/57	1952	5_2	34.409	44	0.433	0.099				
	7/5/58	1953	5_2	34.391	23	0.613	0.167				
	6/29/59	1954	5_2	34.200	15	0.600	0.200				
	7/7/60	1955	5_2	34.521	48	0.680	0.118				
Egegik R.	7/17/56	1952	4_2	34.464	28	0.630	0.148	1.062	2.307	1,122	0.154
	7/11/60	1956	4_2	34.295	95	0.593	0.077				
”	7/17/56	1951	5_3	34.568	111	0.466	0.065	10.018[a,b]	0.202	4,359	0.936
	7/13/57	1952	5_3	34.500	16	0.533	0.189				
	7/7/58	1953	5_3	34.639	97	0.754	0.089				
	7/7/59	1954	5_3	34.552	96	0.839	0.095				
	7/11/60	1955	5_3	34.568	44	0.670	0.122				
”	7/17/56	1950	6_3	34.375	16	1.317	0.296	11.978[a,b]	0.410	4,230	0.798
	7/13/57	1951	6_3	34.481	106	0.614	0.076				
	7/7/58	1952	6_3	34.389	54	0.620	0.108				
	7/7/59	1953	6_3	34.432	44	0.947	0.110				
	7/11/60	1954	6_3	34.666	15	1.067	0.266				
Naknek R.	7/6/56	1951	5_3	34.588	17	0.882	0.228	5.020[a]	0.510	3,263	0.727
	7/9, 13, 19/58	1953	5_3	34.643	70	0.986	0.119				
	7/2/59	1954	5_3	34.486	140	0.669	0.071				
	7/7/60	1955	5_3	34.500	40	1.026	0.161				
”	7/6, 8/56	1950	6_3	34.506	75	0.797	0.105	5.839[a]	2.205	3,426	0.091
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	34.639	316	0.841	0.052				
	7/9/58	1952	6_3	34.765	17	1.066	0.258				
	7/7/60	1954	6_3	34.438	21	0.790	0.195				
Ugashik R.	7/23/56	1952	4_2	34.633	119	0.586	0.140	0.480[a]	2.661	2,318	0.077
	7/19/57	1953	4_2	34.580	30	0.482	0.063				
	7/14/60	1956	4_2	34.401	172	0.592	0.055				

$$C = -2 \sum \ln P_i = 21.080$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

APPENDIX TABLE 5r. Effect of year class on number of ventral gill rakers in sockeye salmon collected in 1956–60.

								F-values			
Area	Date	Year class	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/13/56	1952	4_2	23.100	110	0.770	0.084	1.662[a]	1.359	3,460	0.271
	7/24/58	1954	4_2	22.739	23	1.020	0.215				
	7/9/59	1955	4_2	22.970	33	0.968	0.170				
	7/2, 8, 21/60	1956	4_2	23.124	298	0.931	0.055				
Wood R.	7/11/56	1952	4_2	22.636	118	0.746	0.080	8.993[a,b]	3.453[b]	3,435	0.021
	7/5/58	1954	4_2	22.967	122	0.991	0.090				
	6/29/59	1955	4_2	22.967	123	0.950	0.089				
	7/7/60	1956	4_2	22.711	76	1.382	0.134				
"	7/11/56	1951	5_2	23.089	45	1.219	0.166	6.636[a]	1.753	4,174	0.160
	7/17/57	1952	5_2	22.667	45	0.682	0.124				
	7/5/58	1953	5_2	22.833	24	0.667	0.170				
	6/29/59	1954	5_2	23.063	16	1.127	0.264				
	7/7/60	1955	5_2	23.102	49	0.760	0.126				
Egegik R.	7/17/56	1952	4_2	23.172	29	1.218	0.205	1.569	3.429	1,125	0.065
	7/11/60	1956	4_2	22.806	98	0.776	0.089				
"	7/17/56	1951	5_3	23.045	110	0.888	0.090	0.371[a]	1.908	4,362	0.114
	7/13/57	1952	5_3	23.000	16	0.933	0.249				
	7/7/58	1953	5_3	22.980	99	0.918	0.096				
	7/7/59	1954	5_3	22.796	98	0.824	0.089				
	7/11/60	1955	5_3	22.659	44	0.834	0.138				
"	7/17/56	1950	6_3	22.938	16	0.996	0.258	0.780[a]	2.741[b]	4,230	0.032
	7/13/57	1951	6_3	22.962	106	0.894	0.092				
	7/7/58	1952	6_3	22.630	54	1.068	0.142				
	7/7/59	1953	6_3	23.273	44	0.947	0.148				
	7/11/60	1954	6_3	23.066	15	0.786	0.228				
Naknek R.	7/6/56	1951	5_3	23.125	16	0.517	0.186	3.092[a]	1.556	3,264	0.227
	7/9, 13, 19/58	1953	5_3	22.714	70	0.758	0.105				
	7/2/59	1954	5_3	22.972	142	0.964	0.084				
	7/7/60	1955	5_3	22.950	40	0.818	0.141				
"	7/6, 8/56	1950	6_3	22.883	77	0.947	0.110	1.078[a]	1.014	3,434	0.400
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	23.065	322	0.840	0.051				
	7/9/58	1952	6_3	23.000	18	1.059	0.246				
	7/7/60	1954	6_3	22.857	21	1.028	0.221				
Ugashik R.	7/23/56	1952	4_2	22.966	119	0.880	0.085	1.884[a]	0.461	2,318	0.638
	7/19/57	1953	4_2	22.967	30	1.275	0.206				
	7/14/60	1956	4_2	23.070	172	0.896	0.071				

$C = -2 \sum \ln P_i = 36.406$[c]

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5s. Effect of year class on total number of gill rakers in sockeye salmon collected in 1956–60.

								F-values			
Area	Date	Year class	Age group	Mean	N	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	P
Bristol Bay											
Kvichak R.	7/13/56	1952	4_2	37.391	110	1.396	0.113	6.556[a]	1.701	3,460	0.192
	7/24/58	1954	4_2	36.826	23	2.332	0.326				
	7/9/59	1955	4_2	37.030	33	1.780	0.232				
	7/2, 8, 21/60	1956	4_2	37.372	298	2.080	0.084				
Wood R.	7/11/56	1952	4_2	36.500	118	1.842	0.125	4.462[a]	6.327[c]	3,435	0.001
	7/5/58	1954	4_2	37.157	122	1.901	0.125				
	6/29/59	1955	4_2	37.195	123	1.962	0.126				
	7/7/60	1956	4_2	36.763	76	2.716	0.190				
"	7/11/56	1951	5_2	37.200	45	2.573	0.242	7.062[a]	2.070	4,174	0.089
	7/17/57	1952	5_2	36.578	45	1.431	0.180				
	7/5/58	1953	5_2	37.000	24	1.304	0.238				
	6/29/59	1954	5_2	37.313	16	2.760	0.415				
	7/7/60	1955	5_2	37.306	49	1.592	0.179				
Egegik R.	7/17/56	1952	4_2	37.483	29	2.757	0.308	1.596[b]	6.570[c]	1,125	0.013
	7/11/60	1956	4_2	36.724	98	1.727	0.134				
"	7/17/56	1951	5_3	37.300	110	1.955	0.134	3.597[a]	2.833[b]	4,362	0.025
	7/13/57	1952	5_3	37.188	16	2.029	0.368				
	7/7/58	1953	5_3	37.182	99	1.701	0.132				
	7/7/59	1954	5_3	37.265	98	1.805	0.134				
	7/11/60	1955	5_3	36.545	44	1.184	0.164				
"	7/17/56	1950	6_3	37.250	16	1.400	0.305	1.575[a]	1.957	4,230	0.100
	7/13/57	1951	6_3	37.189	106	1.719	0.128				
	7/7/58	1952	6_3	37.019	54	2.018	0.195				
	7/7/59	1953	6_3	37.705	44	1.794	0.202				
	7/11/60	1954	6_3	37.600	15	1.733	0.340				
Naknek R.	7/6/56	1951	5_3	37.125	16	1.183	0.281	1.487[a]	2.617	3,264	0.052
	7/9, 13, 19/58	1953	5_3	36.471	70	1.992	0.170				
	7/2/59	1954	5_3	36.972	142	1.843	0.114				
	7/7/60	1955	5_3	36.650	40	1.720	0.207				
"	7/6, 8/56	1950	6_3	36.974	77	2.079	0.164	4.032[a]	3.115[b]	3,434	0.026
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	37.338	322	1.651	0.072				
	7/9/58	1952	6_3	37.167	18	2.029	0.346				
	7/7/60	1954	6_3	36.619	21	2.748	0.362				
Ugashik R.	7/23/56	1952	4_2	37.109	119	1.776	0.122	0.281[a]	0.528	2,318	0.402
	7/19/57	1953	4_2	37.367	30	1.965	0.256				
	7/14/60	1956	4_2	37.105	172	1.685	0.100				

$$C = -2 \sum \ln P_i = 57.736^{c}$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

[c] Significant at 1-percent level.

Appendix Table 5t. Effect of year class on number of pectoral fin rays in sockeye salmon collected in 1956–60.

								F-values			
Area	Date	Year class	Age group	Mean	*N*	Variance	Standard error	Variance ratio	Analysis of variance	d. f.	*P*
Bristol Bay											
Kvichak R.	7/13/56	1952	4_2	16.518	110	0.417	0.062	0.868[a]	1.162	3,462	0.332
	7/24/58	1954	4_2	16.409	22	0.348	0.129				
	7/9/59	1955	4_2	16.303	33	0.343	0.100				
	7/2, 8, 21/60	1956	4_2	16.435	301	0.367	0.032				
Wood R.	7/11/56	1952	4_2	16.339	118	0.346	0.054	1.177[a]	0.661	3,436	0.580
	7/5/58	1954	4_2	16.361	122	0.282	0.048				
	6/29/59	1955	4_2	16.270	122	0.315	0.045				
	7/7/60	1956	4_2	16.359	78	0.311	0.063				
"	7/11/56	1951	5_2	16.435	46	0.296	0.081	3.556[a]	1.206	4,175	0.311
	7/17/57	1952	5_2	16.467	45	0.346	0.089				
	7/5/58	1953	5_2	16.583	24	0.341	0.122				
	6/29/59	1954	5_2	16.500	16	0.400	0.158				
	7/7/60	1955	5_2	16.306	49	0.217	0.063				
Egegik R.	7/17/56	1952	4_2	16.686	29	0.607	0.145	2.066[b]	3.223	1,125	0.074
	7/11/60	1956	4_2	16.357	98	0.294	0.055				
"	7/17/56	1951	5_3	16.500	111	0.267	0.133	1.013[a]	0.835	4,362	0.503
	7/13/57	1952	5_3	16.396	16	0.270	0.050				
	7/7/58	1953	5_3	16.556	99	0.252	0.069				
	7/7/59	1954	5_3	16.541	98	0.333	0.055				
	7/11/60	1955	5_3	16.512	43	0.256	0.077				
"	7/17/56	1950	6_3	16.500	16	0.267	0.133	1.311[a]	1.368	4,229	0.262
	7/13/57	1951	6_3	16.396	106	0.270	0.050				
	7/7/58	1952	6_3	16.556	54	0.252	0.069				
	7/7/59	1953	6_3	16.581	43	0.344	0.089				
	7/11/60	1954	6_3	16.466	15	0.280	0.138				
Naknek R.	7/6/56	1951	5_3	16.118	17	0.110	0.026	6.418[a]	1.073	3,262	0.373
	7/9, 13, 19/58	1953	5_3	16.319	69	0.338	0.071				
	7/2/59	1954	5_3	16.193	140	0.301	0.045				
	7/7/60	1955	5_3	16.200	40	0.318	0.089				
"	7/6, 8/56	1950	6_3	16.263	76	0.546	0.084	8.206[a,b]	0.848	3,436	0.474
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	16.268	325	0.363	0.033				
	7/9/58	1952	6_3	16.500	18	0.500	0.171				
	7/7/60	1954	6_3	16.333	21	0.233	0.105				
Ugashik R.	7/23/56	1952	4_2	16.492	120	0.268	0.047	0.777[a]	2.018	2,318	0.155
	7/19/57	1953	4_2	16.333	30	0.327	0.104				
	7/14/60	1956	4_2	16.380	171	0.308	0.045				

$$C = -2 \sum \ln P_i = 22.085$$

[a] Bartlett's test.

[b] Significant at 5-percent level.

Appendix Table 5u. Effect of year class on number of anal fin rays in sockeye salmon collected in 1956–60.

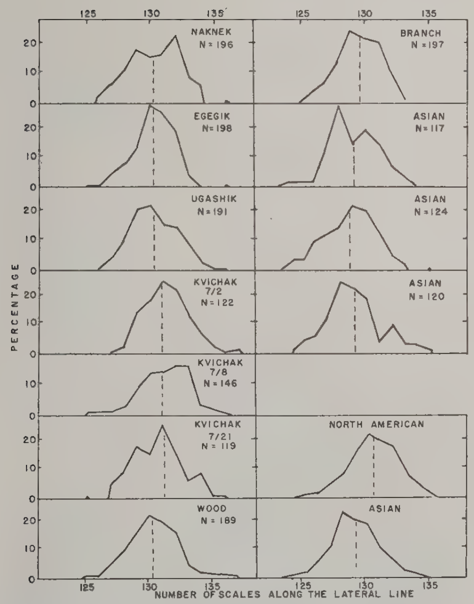
Area	Date	Year class	Age group	Mean	N	Variance	Standard error	F-values		d. f.	P
								Variance ratio	Analysis of variance		
Bristol Bay											
Kvichak R.	7/13/56	1952	4_2	17.862	109	0.435	0.063	0.539^{a}	11.232^{c}	3,461	0.001
	7/24/58	1954	4_2	17.956	23	0.498	0.150				
	7/9/59	1955	4_2	18.091	33	0.398	0.110				
	7/2, 8, 21/60	1956	4_2	18.283	300	0.465	0.045				
Wood R.	7/11/56	1952	4_2	18.008	117	0.474	0.064	5.012^{a}	2.723^{b}	3,433	0.045
	7/5/58	1954	4_2	18.165	121	0.372	0.130				
	6/29/59	1955	4_2	18.246	122	0.451	0.063				
	7/7/60	1956	4_2	18.143	77	0.387	0.071				
"	7/11/56	1951	5_2	18.000	46	0.489	0.104	1.012^{a}	0.767	4,173	0.450
	7/17/57	1952	5_2	18.044	45	0.362	0.091				
	7/5/58	1953	5_2	17.917	24	0.428	0.136				
	6/29/59	1954	5_2	18.200	15	0.457	0.173				
	7/7/60	1955	5_2	18.146	48	0.425	0.095				
Egegik R.	7/17/56	1952	4_2	18.034	29	0.321	0.105	1.151	5.697^{b}	1,125	0.021
	7/11/60	1956	4_2	18.337	98	0.370	0.063				
"	7/17/56	1951	5_3	17.909	110	0.377	0.059	4.581^{a}	7.161^{c}	4,359	0.001
	7/13/57	1952	5_3	18.625	16	0.783	0.229				
	7/7/58	1953	5_3	18.144	97	0.479	0.071				
	7/7/59	1954	5_3	18.010	97	0.470	0.071				
	7/11/60	1955	5_3	18.386	44	0.430	0.100				
"	7/17/56	1950	6_3	18.000	16	0.667	0.211	3.522^{a}	0.872	4,228	0.485
	7/13/57	1951	6_3	18.019	105	0.365	0.059				
	7/7/58	1952	6_3	18.208	53	0.475	0.096				
	7/7/59	1953	6_3	18.045	44	0.370	0.089				
	7/11/60	1954	6_3	18.000	15	0.428	0.167				
Naknek R.	7/6/56	1951	5_3	17.941	17	0.434	0.165	3.408^{a}	1.363	3,263	0.271
	7/9, 13, 19/58	1953	5_3	18.261	69	0.402	0.077				
	7/2/59	1954	5_3	18.121	141	0.407	0.055				
	7/7/60	1955	5_3	18.200	40	0.626	0.126				
"	7/6, 8/56	1950	6_3	17.883	77	0.421	0.071	1.967^{a}	7.388^{c}	3,435	0.001
	7/3, 5, 11, 12, 21, 25, 29/57	1951	6_3	18.034	324	0.497	0.039				
	7/9/58	1952	6_3	18.765	17	0.691	0.208				
	7/7/60	1954	6_3	18.048	21	0.448	0.145				
Ugashik R.	7/23/56	1952	4_2	17.908	119	0.254	0.046	10.456^{a,c}	15.756^{c}	2,318	0.001
	7/19/57	1953	4_2	18.067	30	0.272	0.095				
	7/14/60	1956	4_2	18.302	172	0.434	0.045				

$C = -2 \sum \ln P_i = 74.847^{c}$

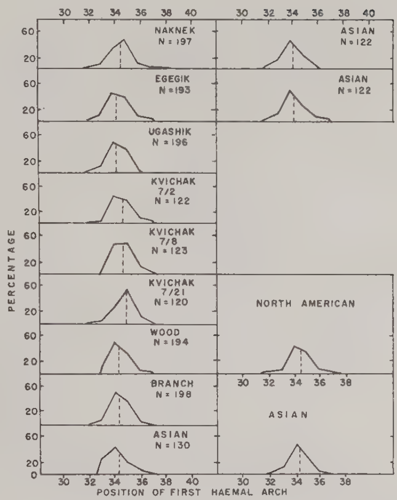
[a] Bartlett's test.

[b] Significant at 5-percent level.

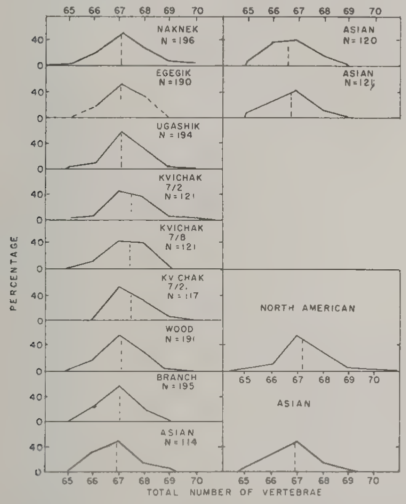
[c] Significant at 1-percent level.



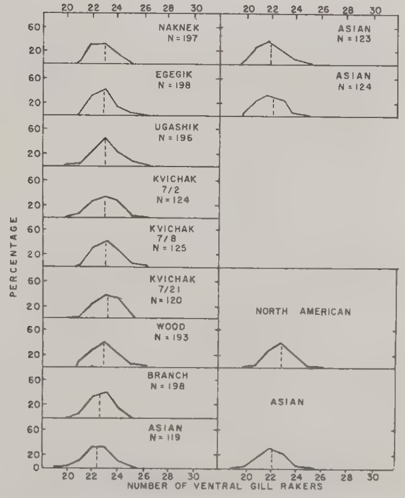
Appendix Figure 1. Percentage frequency distribution of number of scales along the lateral line for 1960 collections of sockeye salmon from Asia and North America which were used as standards for comparison with collections on the high seas. (Broken line shows position of mean, averages for Asian and North American standards are shown in the two lower right panels.)



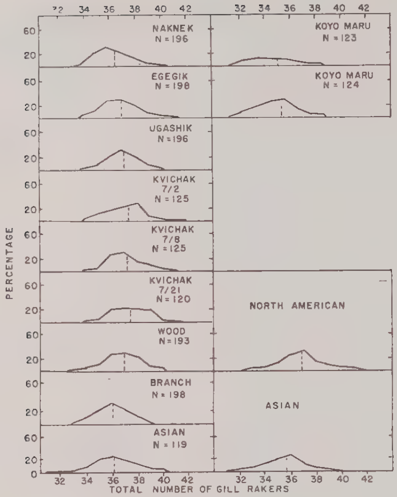
Appendix Figure 3. Percentage frequency distribution of position of the first haemal arch for 1960 collections of sockeye salmon from Asia and North America which were used as standards for comparison with collections on the high seas. (Broken line shows position of mean; averages for Asian and North American standards are shown in the two lower right panels.)



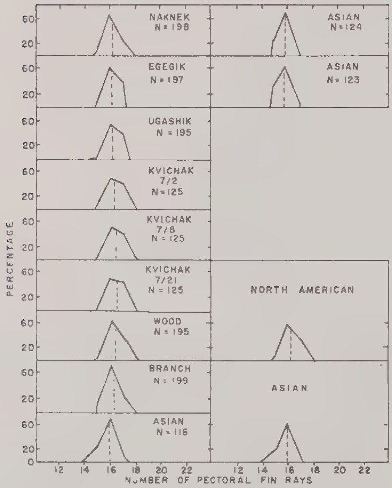
Appendix Figure 2. Percentage frequency distribution of number of vertebrae for 1960 collections of sockeye salmon from Asia and North America which were used as standards for comparison with collections on the high seas. (Broken line shows position of mean; averages for Asian and North American standards are shown in the two lower right panels.)



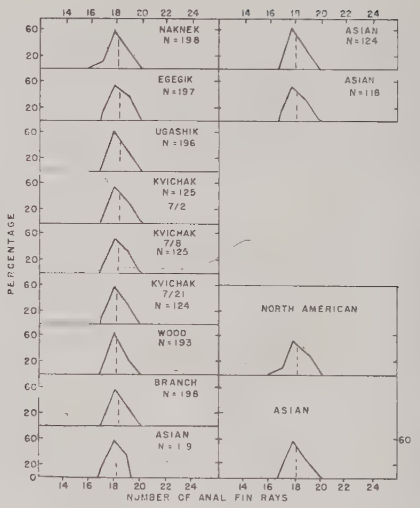
Appendix Figure 4. Percentage frequency distribution of number of ventral gill rakers for 1960 collections of sockeye salmon from Asia and North America which were used as standards for comparison with collections on the high seas. (Broken line shows position of mean; averages for Asian and North American standards are shown in the two lower right panels.)



Appendix Figure 5. Percentage frequency distribution of total number of gill rakers for 1960 collections of sockeye salmon from Asia and North America which were used as standards for comparison with collections on the high seas. (Broken line shows position of mean; averages for Asian and North American standards are shown in the two lower right panels.)



Appendix Figure 6. Percentage frequency distribution of number of pectoral fin rays for 1960 collections of sockeye salmon from Asia and North America which were used as standards for comparison with collections on the high seas. (Broken line shows position of mean; averages for Asian and North American standards are shown in the two lower right panels.)



Appendix Figure 7. Percentage frequency distribution of number of anal fin rays for 1960 collections of sockeye salmon from Asia and North America which were used as standards for comparison with collections on the high seas. (Broken line shows position of mean; averages for Asian and North American standards are shown in the two lower right panels.)

"CHLORIDE CELLS" IN THE SKIN OF THE LARVAL SARDINE

R. LASKER and L. T. THREADGOLD

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"CHLORIDE CELLS" IN THE SKIN OF THE LARVAL SARDINE

R. LASKER and L. T. THREADGOLD

US Bureau of Commercial Fisheries, Fishery-Oceanography Center, La Jolla, Calif. 92037, USA, and Zoology Department, Queens University, Belfast, Northern Ireland

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Since Keys and Willmer [6] suggested that certain acidophilic cells of the fish gill may be osmoregulatory ("chloride secretory"), many workers have tested this hypothesis (see review by Parry [9]). Recent work [14] with the electron microscope has revealed that particular cells in the gills of the salmon, *Salmo salar*, have a unique ultrastructure characterized by smooth-walled tubules ramifying throughout the cytoplasm (often referred to as agranular endoplasmic reticulum e.g. [5, 14]), with subapical microvesicles, numerous mitochondria and a mitochondria-free subapical zone. Distinct changes occurred within these cells when the fish were subjected to sea water after fresh-water adaptation. Observations by others also suggest that acidophil cells of teleost gills play a role in osmoregulation. Getman [2] described changes in the appearance of these cells when fishes were subjected to reversal in osmotic stress, and more recently Philpott [11] demonstrated that only the acidophil cells in the fish gill specifically accumulate halides at their surfaces. Other workers have objected to the "chloride cell" hypothesis of osmotic regulation in teleosts. Parry and Holliday [10] found that pseudobranchs rich in chloride cells could be surgically removed from teleosts without impairing osmoregulatory function and concluded that chloride cells were not essential to osmoregulation. Chloride cells also occur in gills of elasmobranchs which normally rely on urea retention for osmotic regulation [1]. In herring larvae, Jones, Holliday, and Dunn [3] were unable to show changes in the ultrastructure of the larval skin after rearing the larvae in various salinities. Furthermore, despite a comprehensive investigation of the head, yolk sac, and tail, they found no chloride cells. Earlier Holliday and Jones [4] found that developing herring embryos gradually achieve the ability to osmoregulate in the blastula stage.

Larvae of the Pacific sardine (*Sardinops caerulea* Girard) osmoregulate early in their larval development but without having developed the anatomical features later concerned with salt and water regulation in adults, such as gills, an open intestinal tract, functional kidneys and surface scales [7, 8]. If the hypothesis of Keys and Willmer [6] is correct, the early sardine larva should contain chloride cells in its skin, the only differentiated tissue exposed to the environment when active osmoregulation is first observed.

In an earlier investigation [15] we reported on the similarity of certain cells found in larval sardine skin to those described for adult teleost gills as "chloride cells" [11–14]. In this study we describe the larval sardine skin "chloride cell" in detail and present physiological evidence which tends to support the osmoregulatory role for these cells.

MATERIALS AND METHODS

Sardine larvae hatched from eggs in sea water at 18–21°C and varying in length from 4.7 to 6.1 mm were fixed with osmium tetroxide (osmotically adjusted with sucrose) buffered at 7.4, and embedded in Maraglas. Some larvae were put into different sea water salinities before fixation intending to stress their cells osmotically. Four test salinities were chosen: 5 ‰ (hypotonic), 17 ‰ (isotonic), 35 ‰ (hypertonic, normal environment) and 50 ‰ (hypertonic). Individuals were removed from test solutions after 3, 6 and 24 h. The larvae from 17 and 35 ‰ sea water constituted controls. Some embryos were fixed before hatching.

Sections were double stained in uranyl acetate and lead citrate and observed in either an Akashi TRS-50 or an AEI, EM-6B electron microscope. Photographs were taken at 2000 to 10,000 × and enlarged as required.

OBSERVATIONS

"Chloride cells" in the larval skin

Three types of cells were observed in the skin of the larval sardine: (1) the outer epidermal cells, (2) the inner epidermal cells, and (3) the chloride cells which are the particular interest of this paper. The outer and inner epidermal cells are the major elements of the larval skin (Fig. 1); their ultrastructure was described in an earlier paper [15]. The chloride cells are located between the outer and inner epidermal cell layers (Fig. 2) and are found in the yolk sac region of the larva, where they appear to be randomly distributed.

Chloride cells in the skin of the sardine larva are shaped like flattened ellipsoids. Most of them are bounded below by an inner epidermal cell, but in some a small area of the basal plasma membrane contacts the basement membrane (Fig. 3*a*). Outer epidermal cells cover the outer surface of the chloride cell except for a small free area exposed to the environment (Fig. 2). The chloride cells generally have a cytoplasm composed of fine granules and ribosomes widely dispersed over an electron-lucid matrix, which con-

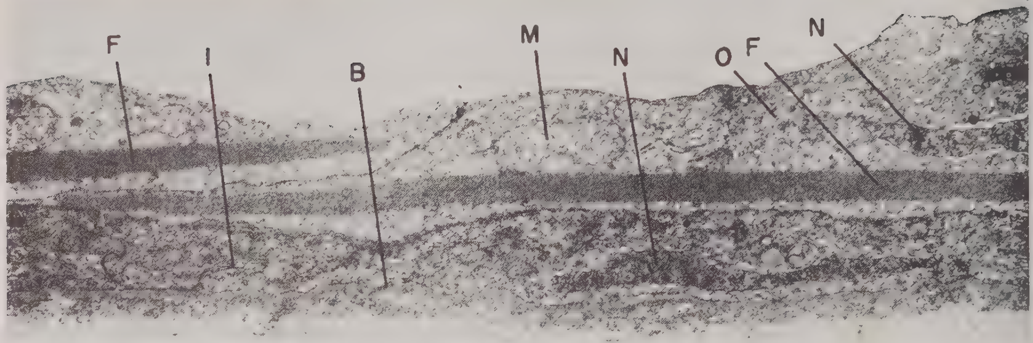

Fig. 1.—An area of the skin of the larval sardine lacking "chloride cells"; inner epidermal cells (*I*) underlie the outer epidermal cells (*O*) which contain a mass of fibers (*F*) whose function is unknown. *B*, Basement membrane; *M*, mitochondrion; *N*, nucleus. ×7150.

trasts with the dense matrices of the adjacent outer and inner epidermal cells. The cytoplasm below the exposed outer plasma membrane is, however, more dense than the remainder of the cytoplasm because of a concentration of granules and small vesicles (Fig. 2, insert). The cytoplasm of the chloride cell contains a ramifying network of smooth-walled tubules, which may arise from any point on the plasma membrane. Sections of the tubules are close to, or in contact with, the region of the plasma membrane exposed to the environment. Non-tubular cisternae and vacuoles of irregular shape, all without ribosomes, are randomly distributed throughout the cytoplasm of the chloride cells (Fig. 3*a*).

The chloride cell has a number of large mitochondria, which generally are concentrated beneath the exposed plasma membrane (Fig. 2). The mitochondria have light matrices and many villous cristae which project into the matrix at all angles and overlap.

In various sections not shown here, the nucleus of the chloride cell tends to lie laterally and is usually long and undulant, but sometimes may be compact and oval. The nuclear membrane encloses a homogeneous granular nucleoplasm (Fig. 3*b*).

Effect of salinity stress on skin and chloride cells

Both skin and chloride cells changed in dimension when subjected to salinity stress. Measurements were made of skin cell thickness from cross

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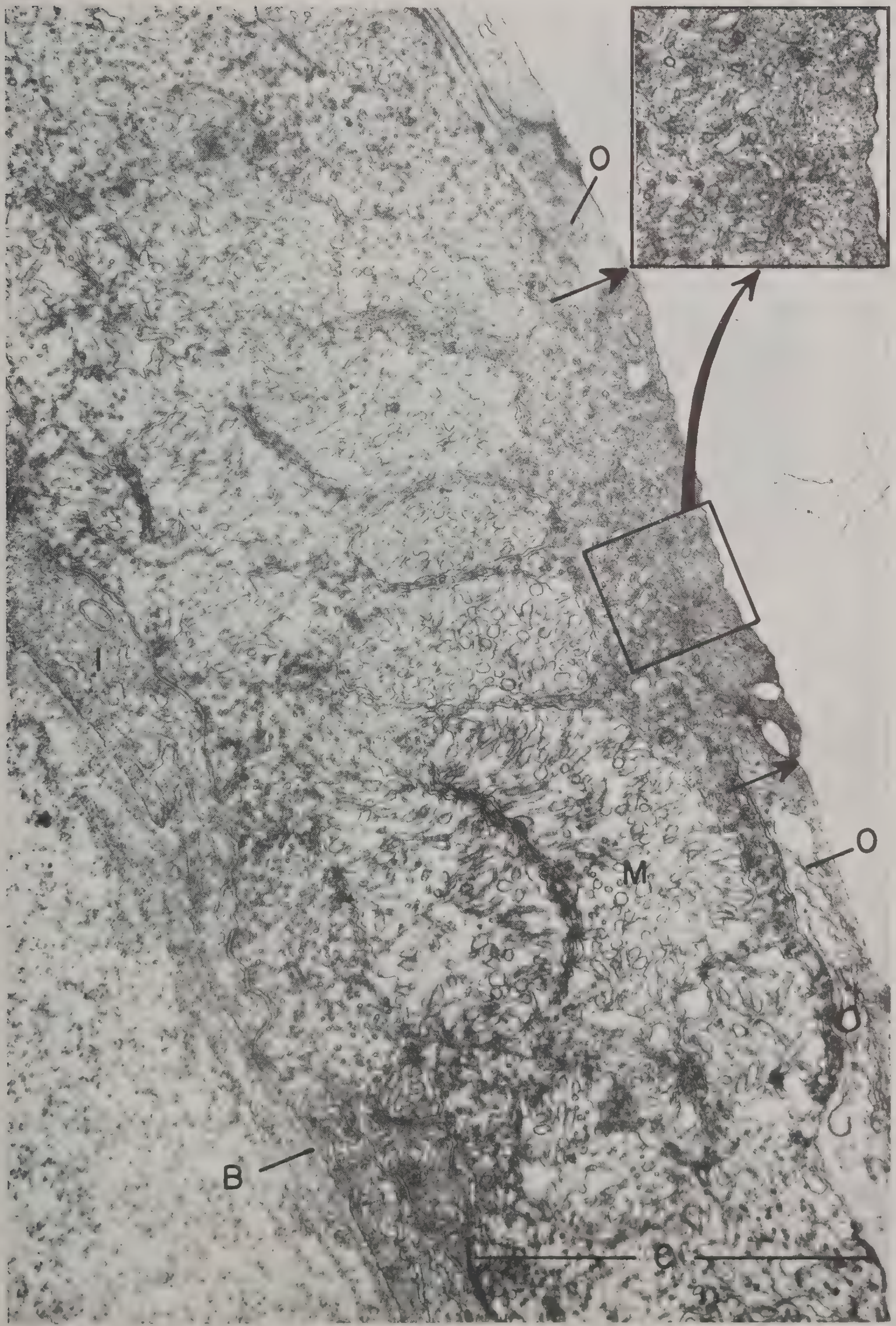
Fig. 2.—A "chloride cell" from the larval sardine skin. Its base lies on an inner epidermal cell (*I*) and its outer surface is overlain by outer epidermal cells (*O*), except for an area between the straight arrows which is exposed to the environment. ×16,860. The insert is an enlarged part of the exposed area and its adjacent cytoplasm. ×24,960. *M*, mitochondrion; *B*, basement membrane; *C*, chloride cell.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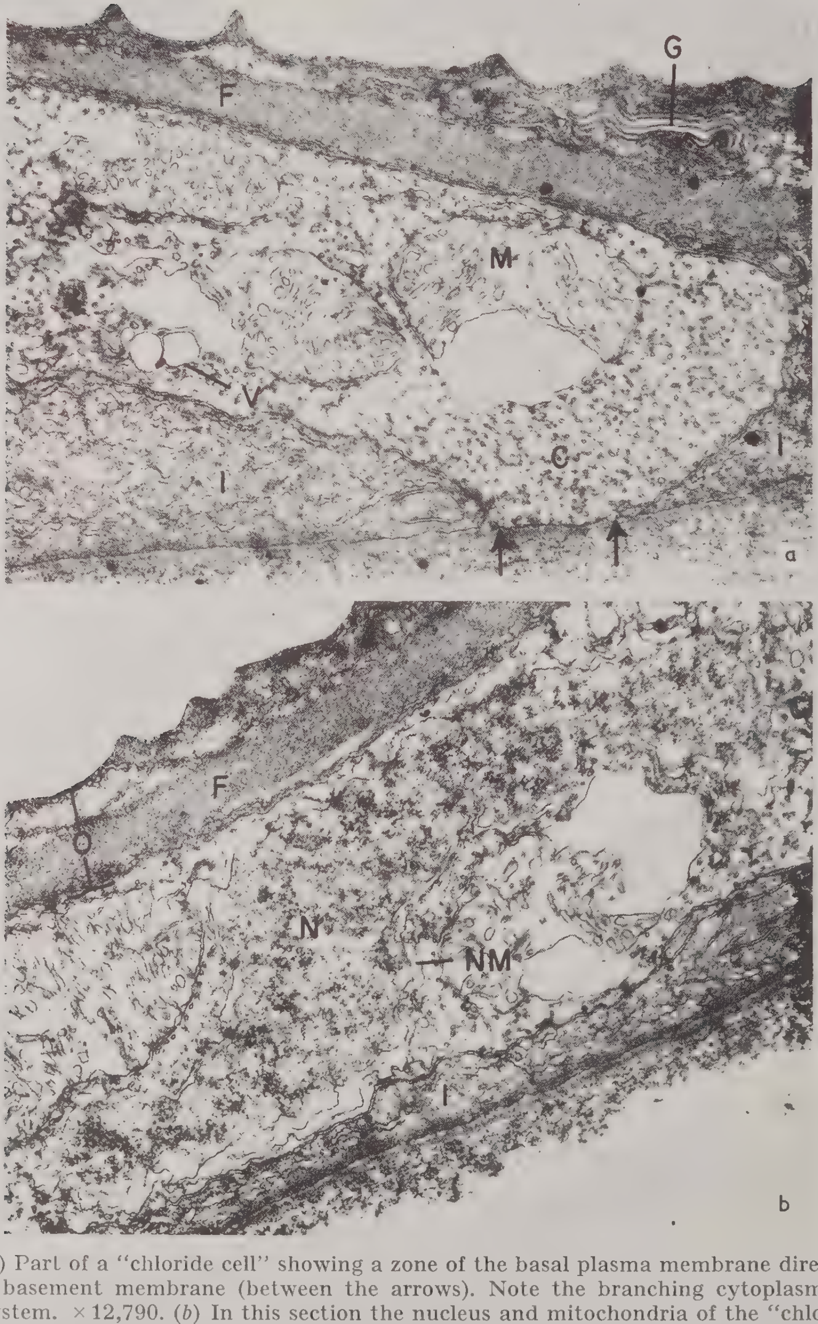

Fig. 3—(*a*) Part of a "chloride cell" showing a zone of the basal plasma membrane directly overlying the basement membrane (between the arrows). Note the branching cytoplasmic microtubular system. ×12,790. (*b*) In this section the nucleus and mitochondria of the "chloride cell" are shown. ×15,380. *C*, chloride cell. *F*, dense mass of fibers. *G*, golgi complex. *I*, inner epidermal cell. *M*, mitochondrion. *N*, nucleus. *NM*, nuclear membrane. *O*, outer epidermal cell. *V*, vacuole.

sections where there were no chloride cells. Because the chloride cells are elliptical, the thickness of each was measured at its widest portion in transverse section.

There was an initial swelling of the skin and chloride cells in both 5‰ and 50‰ solutions, followed by a return to near-normal in 6 h by the skin cells (Fig. 4). Chloride cells continued to swell even after the skin cells returned to normal but all cells had returned to near-normal dimensions by 24 h. In 17‰ and 35‰ salinities no discernible changes occurred.

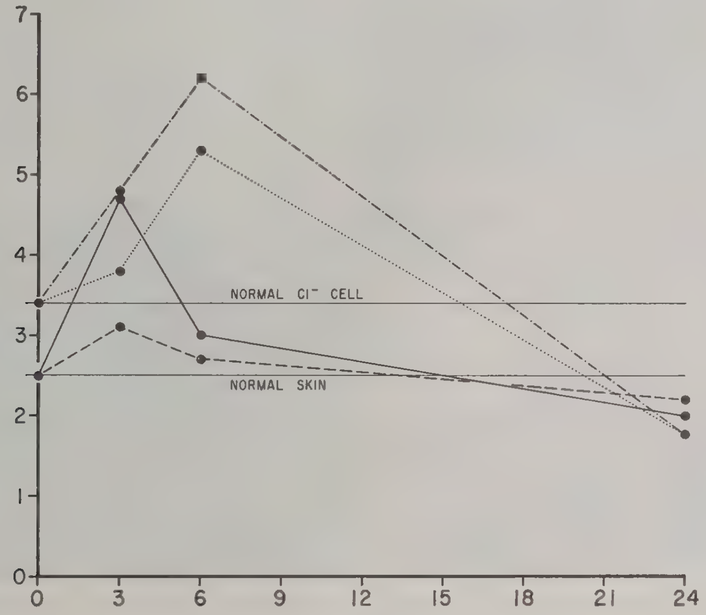

Fig. 4.—Change in thickness with time of sardine larval skin and "chloride cells" at different salinities. "Normal" lines refer to thickness at 17 and 35‰ which did not change with time. *Abscissa:* Time (h); *ordinate:* cell thickness (μ). · — · — ·, 5‰ Cl cell; · · · · ·, 50‰ Cl-cell; ——, 5‰ skin; – – – –, 50‰ skin.

Only the chloride cells of the skin showed ultrastructural changes when subjected to hypo- and hyper-tonic solutions of sea water. Fig. 5 illustrates the differences seen in the micro-tubular structure of chloride cells responding to extreme tonicities as compared with those of 17‰ and 35‰ sea water. After 24 h in 50‰, the micro-tubules increased in diameter and crammed the cytoplasm of the cell. In hypotonically-treated larvae there was an initial dilution of chloride cell cytoplasm, the tubules becoming markedly thinner in diameter; however, after 24 h the micro-tubules returned to the size characteristic of an unstressed chloride cell.

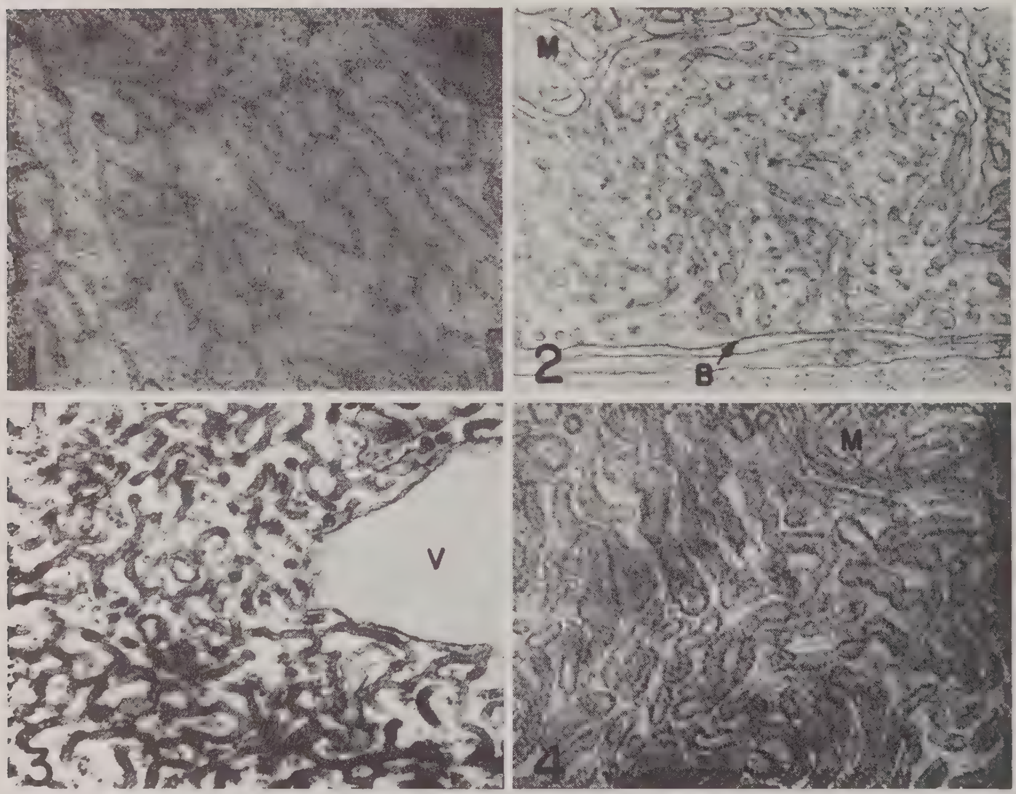

Fig. 5.—Micro-tubular structure of "chloride cells" at different salinities. (1) 5 ‰ salinity, 3 h, (2) 17 ‰, 24 h; (3) 35 ‰, 24 h; (4) 50 ‰, 24 h. *M*, mitochondria; *B*, basement membrane; *V*, vacuole; × 41,870.

Interpretation of the salinity stress experiments reported here in the context of the chloride cell hypothesis is difficult The swelling of skin cells and their early return to normal suggest that they might have an innate ability to osmoregulate without chloride cell mediation, as suggested for herring embryos [3]. However, in salinity stressed sardine larvae the ultrastructure was altered significantly only in chloride cells. The delay in chloride cell volume reduction, as compared to the skin cells might be interpreted as an osmoregulatory response, alleviating the extreme water and salt conditions in the surrounding cells.

DISCUSSION

The organization and ultrastructure of the skin of the larval sardine closely resembles that of the larval herring, as described by Jones, Holliday and

Dunn [3]. The major difference between the structure of the skin of the sardine and the herring is the presence in the sardine of a third cell type, the chloride cell. On the basis of their ultrastructure, larval skin chloride cells appear to be similar to chloride secretory cells of the gills of salmon [14], of the guppy [13], of three species of *Fundulus* [5, 12], and of a mouth breeder, *Tilapia macrocephala*, and the elasmobranch, *Urobatis* sp. [1]. The characteristic ultrastructural features of all chloride cells described thus far are the presence of numerous mitochondria, a branching system of smooth-walled tubules, and a localized area of the free outer plasma membrane exposed to the environment.

Lasker and Theilacker [8] demonstrated that the larvae of sardines do osmoregulate. Since larvae lack functional kidneys, a mouth or gills during the yolk sac period, Lasker and Theilacker [8] postulated that the cells of the skin may perform this function. In the present study chloride cells were found in all areas of the skin overlying the yolk of the sardine larva, although not in its tail or head. Dechorionated eggs do not osmoregulate as effectively as older larvae [7], and we were not able to find chloride cells in the embryonic stages of the sardine within the egg. We therefore suggest that, because of their ultrastructural morphology, the changes in micro-tubular structure and cell volume with salinity stress, position within the larval skin, and time of appearance, chloride cells of the larval sardine may be concerned with osmoregulation.

SUMMARY

Cells resembling ultrastructurally the "chloride cells" of teleost gills were found in the skin of the undeveloped, larval sardine. These cells are characterized by a branching system of smooth-walled tubules, numerous mitochondria and exposure to the environment by a localized area of the outer plasma membrane. Salinity stress alters the ultrastructure of the "chloride cells" but not of the surrounding skin cells. Increases of cell volume occurred in 5 and 50‰ salinities, with skin cells showing smaller fluctuation than chloride cells, the latter returning to normal later than the former.

We thank the Wellcome Trust for a grant to purchase an Akashi TRS-50 electron microscope, the Royal Society for a Reichert Ultramicrotome, and the D.S.I.F. for an AEI EM-6B electron microscope. We acknowledge with thanks the technical assistance of Mr A. Lyness, Mrs Gail H. Theilacker and Miss Christine Bowker.

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Effect of Temperature and Salinity on the Survival of Young Atlantic Menhaden, *Brevoortia tyrannus*

Robert M. Lewis and William F. Hettler, Jr.

Effect of Temperature and Salinity on the Survival of Young Atlantic Menhaden, *Brevoortia tyrannus*

ROBERT M. LEWIS AND WILLIAM F. HETTLER, JR.
Bureau of Commercial Fisheries, Biological Laboratory, Beaufort, North Carolina

ABSTRACT

Survival of young Atlantic menhaden at different salinities and temperatures was studied in the laboratory. Fish were tested in the spring, summer, and early fall at high temperatures (25 to 36 C) and low (5 to 7‰), intermediate (15‰), and high salinities (31 to 34‰). In the late fall and early winter, tests were conducted at temperatures of 3 to 7 C and salinities of 10 and 26 to 30‰. Temperature had the greatest effect on survival; acclimation time also affected survival but to a lesser degree. Salinity did not appear to markedly affect survival time at the temperatures studied. Yearlings were more sensitive to high temperatures than were younger fish.

INTRODUCTION

Investigation of the response of young Atlantic menhaden to different levels of environmental factors forms one phase of research at the Bureau of Commercial Fisheries Biological Laboratory in Beaufort, North Carolina. Extremes in temperature and salinity encountered in estuarine waters probably contribute to natural mortality in menhaden populations and may be conjectured as being at least partly responsible for fluctuations in year-class strength. Temperature and salinity probably also affect the distribution of young menhaden within an estuary. In some estuaries avoidance of adversely high water temperatures by fish and shellfish is becoming increasingly difficult as industry discharges increasingly greater volumes of heated waste water (Mihursky and Kennedy, 1966).

A series of laboratory experiments was begun in the spring of 1966 to determine whether high or low water temperatures, salinity, and their interaction materially affect the survival of young menhaden. Field records suggested that menhaden collected in South Carolina estuaries withstood 36 C water temperatures. Salinities of the nursery areas for young menhaden vary from 0 to 40‰. In this study we tried to simulate the upper (or lower) ranges of temperature and salinity to which young menhaden might be exposed in their natural environment. For example, in the late spring and summer when water temperatures are fairly high, we tested fish at temperatures of 25 C or greater; in the late fall when water temperatures drop rapidly, tests were conducted at 7 C and below. In addition, we examined the effects of (1) acclimation time, (2) rate of change from acclimation temperature to test temperature, (3) oxygen concentration, and (4) the effect of a common parasite on the gills. The present work follows earlier studies of the tolerance by larval Atlantic menhaden to low temperatures at different salinities (Lewis, 1965 and 1966).

EXPERIMENTAL MATERIAL AND PROCEDURES

Young menhaden were collected as needed in the vicinity of Beaufort, North Carolina. Young-of-the-year were collected in a small pound net and with a haul seine from the lower Neuse River (a low-salinity area) and yearlings with a haul seine from Broad Creek (a high-salinity area). The young-of-the-year ranged from 33 to 109 mm and yearlings from 138 to 194 mm total length. The fish were transported to the laboratory in a 125-gallon tank. As the trip took less than 1 hour the water was not aerated or recirculated. At the laboratory, fish were placed in an acclimation tank with continuous flowing water and held at least 3 to 4 days until handling mortality subsided. All water used to acclimate or test the fish was pumped from the Beaufort Harbor. When we needed lower salinity water, fresh water from the laboratory well was added to dilute the harbor water.

The experimental layout consisted of a 600-gallon, circular fiberglass acclimation tank and three, 25-gallon, plastic-lined metal

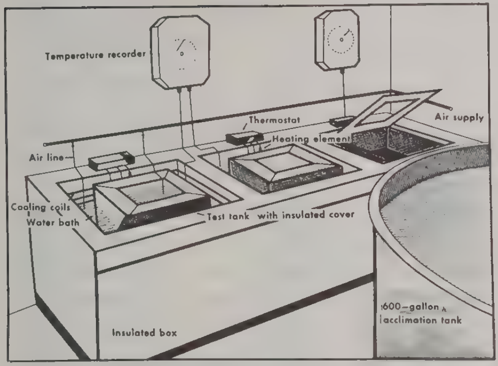

FIGURE 1.—Experimental layout for the study of the effects of temperature and salinity on young menhaden.

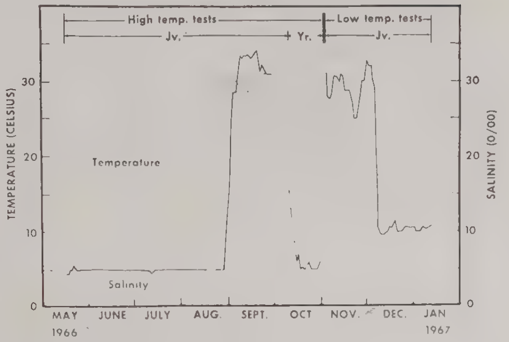

FIGURE 2.—Temperatures (dotted line) and salinities (solid line) of water in the tank at which young-of-the-year and yearling Atlantic menhaden were acclimated during experiments.

test tanks (Figure 1). A Thermistemp and thermistor probe made by Yellow Springs Instrument Company[1] regulated the temperature in each test tank. During acclimation, fish were fed a powdered fish ration or *Artemia* nauplii. Feeding continued during a test as long as the test fish accepted food.

As we had no prior knowledge of the upper lethal temperatures for young-of-the-year Atlantic menhaden, we ran preliminary tests to determine at what temperature stress occurs. Fish were acclimated at least 1 week to temperatures of 20 to 23 C and then tested at 25, 30, and 35 C. Salinity of acclimation and test waters was about 5‰. No significant mortality occurred at 25 or 30 C, but all fish died in less than 15 hours at 35 C.

Additional tests were run at 5‰ salinity and temperatures of 32, 33, and 34 C, levels commonly observed during the summer in estuarine areas known to harbor concentrations of young menhaden. No significant mortality occurred at 32 or 33 C, but at 34 C 50% of the test fish died within 5 days. These preliminary tests indicated that temperatures near 35 C would provide us with a working base from which to further delimit the relations between temperature, salinity, and acclimation time and the effect of these variables on survival time.

During the late spring and summer young-of-the-year menhaden generally are found on nursery grounds where the salinity is 5‰ or less. By fall and winter most young menhaden return to high salinity waters of the lower estuary. In our experiments, acclimation conditions in the tank were controlled so that salinity and temperature were similar to those of the water from which the fish had been collected (Figure 2). The acclimation time varied considerably because we lacked additional acclimation tanks and fish were not always available. The acclimation history is as follows: From the middle of May to the end of August fish were held in water at approximately a 5‰ salinity and a temperature of 20 to 23 C. During October, November, and December fish were held at low (5 to 7‰), medium (15‰) and high (25‰ and greater) salinities and at temperatures between 8 and 25 C. These conditions simulate the ranges which young menhaden encounter in their natural environment. In September we acclimated fish at a salinity of 30‰ and a temperature of 30 C to determine if these acclimation levels had any effect on survival at high test temperatures.

On initiating each experiment we filled the test tanks with water from the acclimation tank so that the 10 young-of-the-year (or 5 yearlings) in each test would not suffer temperature or salinity shock when introduced. The rate of change from acclimation to test temperature was different in the high- and low-temperature tests. In the high-temperature

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[1] Trade names referred to in this publication do not imply endorsement.

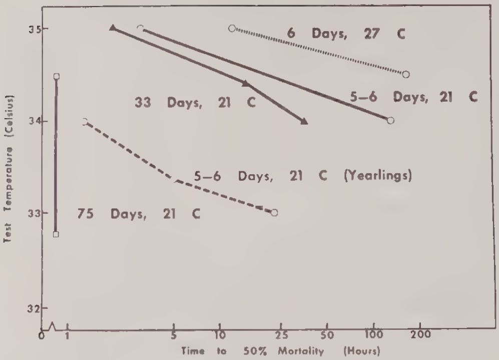

FIGURE 3.—Upper lethal temperature relations for juvenile and yearling Atlantic menhaden. Each point on a line represents one test with 10 young-of-the-year or 5 yearling fish. Resistance time lines for juveniles acclimated to 21 C for 5–6, 33, and 75 days (solid line); young-of-the-year acclimated to 27 C for 6 days (dotted line); and yearlings acclimated to 21 C for 5–6 days (dashed line). Salinity for the acclimation and test periods was 5‰.

tests this change was linear at about 1 degree per hour. In the low-temperature tests it was nonlinear; for example, 2 hours were required to lower the temperature from 18 to 6 C, and 5 hours to lower it from 6 to 4 C. Compressed air bubbled through the water kept the oxygen level in the experimental tanks at about 100% saturation. We continued each test and its control until 50% mortality had occurred or at least 7 days had elapsed.

EFFECTS OF TEMPERATURE AND SALINITY

Young-of-the-year menhaden are very active and difficult to touch with a probe when held at temperatures between 20 and 30 C. At temperatures above 30 C, they swim near the surface with their heads up, gulp air, stop schooling, are less active, and can easily be touched with a probe. With continued exposure they lose stability, start swimming on their sides, settle to the bottom, and occasionally swim in spurts. The amount of swimming decreases progressively. Finally, they lie on the bottom of the tank and flex their opercula at infrequent intervals until death occurs.

Responses in young-of-the-year menhaden were similar at lethal low temperatures to those at high temperatures, although attenuation of breathing spanned a greater amount of time than during high-temperature tests. When held 1 or 2 degrees C below the stress level for 1 week, their body coloration changed from silvery to white.

Results of high-temperature and 5‰ salinity tests revealed that acclimation temperature as well as acclimation time strongly influenced the survival of young-of-the-year (Table 1).

The relations between test temperature and time to 50% mortality were similar for young-of-the-year acclimated from 5 to 21 days, but changed markedly for fish acclimated 33 days (Figure 3). Acclimation of fish for progressively longer periods appeared to reduce survival at each test temperature. Fish acclimated for 75 days survived less than 1 hour at the high test temperatures. When the acclimation temperature was raised from 21 to 27 C and the acclimation time was held uniform at about 6 days, the tolerance of young-of-the-year to high temperatures increased.

In tests run at comparably high temperatures, but at a salinity of 15‰, survival was similar to that in the low-salinity tests (Table 1).

In another series of tests at high temperatures and salinities of 31 to 34‰, survival time was significantly reduced as the test temperature was increased (Table 1). Young-of-the-year menhaden survived longer than 6 days at 34.3 C but only 1-½ days or less at higher temperatures (only a few hours at temperatures above 35.5 C). On the basis of the low-, medium-, and high-salinity tests it appears that salinity is not an important factor in modifying survival at high temperatures.

We also conducted tests with yearling menhaden that had been acclimated at a low salinity (5‰) for 4 to 20 days (Table 2). Fish survived 5 or more days at temperatures below 32 C but only 1 day or less at temperatures above 32.8 C. When fish were acclimated from 5 to 6 days at 21 C, the results indicated that young-of-the-year tolerated higher temperatures than did yearlings (Figure 3).

In late fall, as the water temperature of the natural environment cooled, young-of-the-year menhaden were tested at 3, 4, 5, 6, and 7 C, and at 10 and 26 to 30‰ salinity (Table 3). Acclimation temperature varied between 7.5 and 20.0 C (Figure 2). At 26 to 30‰ salinity,

TABLE 1.—*Results of tests with young-of-the-year Atlantic menhaden subject to high temperature at low, medium, and high salinities*

Test		Acclimation			Hours after start of experiment			
Temperature Celsius	Salinity ‰	Number of hours	Median temperature Celsius	Median salinity ‰	First death	50% survival	Last death	Termination
25.0	5	100–500	22	4	–[1]	–	–	237
30.0	5	100–500	22	4	40	–	–	211
32.0	5	100–500	22	5	–	–	–	154
33.0	5	100–500	21	5	130	–	–	161
33.8	5	>500	21	4	<1	1	2	2
34.0	5	100–500	21	5	12	132	–	161
34.0	5	100–500	27	5	–	–	–	172
34.0	5	100–500	21	4	48	–	–	185
34.0	5	>500	21	4	24	36	107	107
34.2	5	>500	21	4	<1	<2	3	3
34.4	5	>500	21	4	3	15	27	27
34.5	5	100–500	27	5	14	–	–	168
34.5	5	100–500	21	4	46	100	–	168
34.5	5	>500	21	4	<1	<1	3	3
34.5	5	>500	21	4	<1	<1	<1	<1
34.8	5	>500	21	4	<2	<2	3	3
35.0	5	100–500	27	5	10	12	22	22
35.0	5	100–500	21	4	<1	<3	8	8
35.0	5	100–500	21	4	3	<4	6	6
35.0	5	>500	21	4	<1	<1	3	3
35.0	15	<100	24	15	2	<5	7	7
35.5	15	<100	24	15	3	<4	4	4
35.5	15	100–500	24	15	<1	<2	2	2
36.0	15	<100	24	15	<1	<1	1	1
34.3	32	100–500	29	30	–	–	–	158
34.8	32	100–500	29	30	6	32	77	77
35.0	32	100–500	29	30	33	36	85	85
35.2	32	100–500	29	33	7	8	24	24
35.5	34	100–500	29	33	5	8	21	21
35.7	31	100–500	29	32	5	6	8	8
36.0	33	100–500	29	32	3	3	4	4
36.5	31	100–500	29	32	1	<2	2	2

[1] Dashes indicate no deaths.

survival was longer than 5 days at or above 6.0 C, about 2 days at 5.0 C and 1 day or less at or below 4.0 C. At 10‰ salinity fish survived 4 or more days at 5.0 C, and 2 days or less at or below 4.0 C. A comparison between both series of tests indicated that at low temperatures salinity has a limited effect on survival.

The combined results of the tests on young menhaden at high and low temperatures indicated that salinity affects survival less than does temperature. This observation compares with the findings of Lewis (1966) who showed that larval menhaden also have a wide salinity tolerance. Even though menhaden may survive in a wide range of salinities, they probably respond to salinity gradients in an estuary or river that may act as cues to guide them to

TABLE 2.—*Results of tests with yearling Atlantic menhaden subjected to high temperatures at low salinities*

Test		Acclimation			Hours after start of experiment			
Temperature Celsius	Salinity ‰	Number of hours	Median temperature Celsius	Median salinity ‰	First death	50% survival	Last death	Termination
31.0	6	100–500	22	7	40	–[1]	–	136
31.0	6	100–500	22	7	–	–	–	136
31.0	6	100–500	22	7	–	–	–	136
31.5	5	100–500	22	7	82	–	–	130
31.9	5	100–500	22	7	38	73	131	131
32.0	5	100–500	22	7	10	18	87	87
32.8	5	100–500	23	7	4	4	28	28
33.0	5	100–500	23	7	7	23	–	64
33.3	5	100–500	23	7	4	5	28	28
34.0	5	100–500	23	7	<1	2	4	4
34.0	5	100–500	23	7	1	1	4	4
34.0	5	100–500	23	7	1	2	6	6
34.0	4	<100	23	7	<1	<2	4	4
35.0	4	<100	23	7	<1	<1	<1	<1

[1] Dashes indicate no deaths.

TABLE 3.—*Results of tests with young-of-the-year Atlantic menhaden subjected to low temperatures at low and high salinities*

Test		Acclimation			Hours after start of experiment			
Temperature Celsius	Salinity ‰	Number of hours	Median temperature Celsius	Median salinity ‰	First death	50% survival	Last death	Termination
7.0	27	>500	12	28	–[1]	–	–	128
7.0	30	>500	15	28	118	–	–	160
6.0	30	>500	15	28	40	160	–	231
6.0	30	>500	15	28	141	234	–	256
5.0	26	100–500	16	29	39	61	98	98
5.0	26	100–500	16	29	40	53	98	98
4.0	26	100–500	16	29	16	28	37	37
4.0	27	100–500	16	29	3	16	–	21
3.0	27	100–500	16	29	5	10	16	16
3.0	27	100–500	16	29	3	6	11	11
7.0	10	>500	18	10	235	–	–	358
6.0	10	>500	18	10	86	149	–	334
5.0	10	>500	18	10	110	110	–	142
5.0	10	100–500	18	10	128	170	240	240
5.0	10	100–500	18	10	100	114	191	191
4.0	10	>500	18	10	24	27	63	63
4.0	10	100–500	18	10	6	6	99	99
4.0	10	100–500	18	10	23	49	98	98
3.0	10	100–500	18	10	>1	3	49	49
3.0	10	100–500	18	10	0	2	28	28

[1] Dashes indicate no deaths.

and from their nursery areas. McInerney (1964) established that the sequence of changes in preferred salinities paralleled the salinity gradients typical of river outflows through which young salmon pass on their way to the ocean.

The difference in temperature tolerance between young-of-the-year tested in the spring and summer and yearlings tested in the fall cannot be explained by variation in acclimation temperature because both groups of fish were acclimated at similar temperatures (Figure 2). Instead, this difference reflects a developmental change in young menhaden, or a seasonal change regulated by daily photoperiod, or both. Investigations of other species have usually shown that differences in temperature tolerance were associated with a seasonal change rather than a developmental change. For example, preferred temperatures of *Salvelinus fontinalis* (Sullivan and Fisher, 1953) and the thermal resistance of *Carassius auratus* (Hoar, 1955), have been shown to vary seasonally during the year independent of temperature changes or acclimation temperatures. Subsequent tests by Hoar (1956) and Hoar and Robertson (1959) revealed that goldfish reared for short photoperiods were more resistant to low temperatures than those reared at long photoperiods, whereas the reverse was true at high temperatures. Therefore, because we found differences in thermal tolerance between young menhaden tested in spring-summer and in the fall, the observed thermal difference probably reflected a seasonal change in thermal tolerance rather than a physiological change associated with development.

RATE OF TEMPERATURE CHANGE

The rate of temperature change from acclimation to test temperature was examined to determine its effect on survival. In June 1966, 20 fish were tested to determine if young-of-the-year menhaden, acclimated to a salinity of 5‰, could recover from heat stress. The water temperature was raised from the acclimation temperature of 23.0 C (at which the fish had been held 1 month) to 34.8 C in 2 hours. When the fish showed signs of stress at this high temperature, the temperature was lowered in 1 hour to its former level. Six of the 20 fish survived the experiment.

We acclimated another group of 20 fish at 5‰ and 22.5 C ± 1.0 C for 1 month and then raised the temperature approximately 1 degree per day until it reached 35 C to determine if the rate of temperature change affected survival. Fifty percent of the fish survived 20 hours as compared with 1-½ hours for fish brought to this test level in only 13 hours.

EFFECT OF OXYGEN ON SURVIVAL

Young-of-the-year menhaden were held at 35.5 C, after acclimation for 1 week at 24 C, and tested twice to determine if oxygen concentration affects survival. In the first test, compressed air maintained the test medium at 100% saturation; 5 of the 10 fish survived 1-½ hours. In the second test the oxygen level was kept at 400‰ saturation; half of the fish survived 3 hours. Oxygen concentration apparently can play an important part in controlling survival of young-of-the-year menhaden at high temperatures.

EFFECT OF A PARASITE ON MENHADEN

Olencira praegustator, an isopod, parasitizes both Atlantic menhaden and Gulf menhadens, *Brevoortia patronus* and *B. smithi.* Turner and Roe (1967) reported that most of their parasitized fish contained a single large isopod attached to the anterior roof of the mouth, and that some fish also contained a small isopod attached to the gill filaments. In Albemarle Sound, North Carolina, the incidence of this menhaden parasite is so common that commercial fishermen refer to the fish as "bugmouths."

Turner and Roe (1967) also noted a small amount of gill erosion in some of the fishes but saw no indication that the condition of the host was affected. To determine if the erosion caused by the parasite had any effect on survival time, we conducted two tests with 5 fish each at 34 C to compare survival of unparasitized fish with survival of fish that bore parasites and had erosion of the gills. Gill condition was a factor affecting survival: 50% of the fish with healthy gills survived 2 hours as compared to 1 hour for those with eroded gills.

SUMMARY

The results of the present study revealed that high temperature has a pronounced effect on the survival of young menhaden. Temperatures above 33 C are not uncommon in menhaden nursery areas during the summer and, with more power plants discharging heated waste water, high water temperatures will become an increasing threat to young menhaden.

Acclimation time and temperature, salinity, oxygen level, and gill condition are some of the components that determine how long young menhaden will survive at a particular test temperature, in the laboratory. Test temperatures above 33 C caused death in young menhaden. How soon they die at these high test temperatures depends in part on the levels of the acclimation factors. For example, if the temperature was raised gradually to the test temperature over a period of several days, fish survived longer than if the test temperature was reached in a few hours. This means that if the water temperature in a nursery area increases gradually, menhaden have a better chance to survive than if they are trapped in a discharge of heated water. The condition of the fish and the amount of oxygen present in the water will also determine how long fish survive when subject to adverse thermal conditions.

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DISTRIBUTION OF THE LARVAE OF *PLEURONCODES PLANIPES* IN THE CALIFORNIA CURRENT

Alan R. Longhurst[1]
Institute of Marine Resources, Scripps Institution of Oceanography,
University of California, San Diego

ABSTRACT

Zoeae and megalopas of *Pleuroncodes planipes* Stimpson were found in 483 of 2,546 plankton samples from the California Current in 1957 and 1959. Their distribution in the samples showed that 1) breeding occurred during winter, mostly in February and March; 2) while some breeding could be ascribed to offshore pelagic adults, the greatest larval concentrations were over the continental shelf, often only in the presumed presence of benthic adult populations; 3) breeding extended far to the north of the usual range in the warm years centered around 1959, though it was probably not successful in the extreme north; and 4) there was clear evidence of late zoeae and megalopas being carried offshore in accordance with known geostrophic flow patterns so that at least a high proportion of megalopas had the possibility of changing to the benthic phase only after an excursion into oceanic regions. The data cannot be used to decide whether 5) any of these megalopas do, in fact, achieve a return to the coast or whether 6) any megalopas descend directly into the benthic phase after metamorphosis over the continental shelf.

INTRODUCTION

Pleuroncodes planipes Stimpson is one of the few species of galatheid crabs in which the pelagic habit may be extended from larval into adult life, or may recur in adult life after a period of benthic existence; both in the pelagic and the benthic phase the species is extremely abundant in the southern part of the California Current, where it forms the major item in the diet of commercially important tropical tunas during their summer migration into the region. The general biology of *P. planipes* has recently been reviewed by Boyd (1963, 1967) and by Longhurst (1967*a*, *b*).

The species passes through five larval stages, each comprising a single instar except the fourth, in which from four to eight instars may be passed; the larval stages have been described by Boyd (1960) and Boyd and Johnson (1963). There are, of course, other galatheids in the region and the possibility of confusion between the larvae of these and of *P. planipes* does exist, the more so since the larvae of the species concerned have not themselves been described; these are a species of *Galathea*, two of *Munida*, and four of *Munidopsis* (Schmitt 1921). Since the planktonic larvae of several species of the first two genera have been described from other regions and have proved to have characteristics generally distinct from those of *P. planipes*, and because the third genus is likely to have larvae rather distinct from those of the other genera, it is reasonable to make certain assumptions about the identity of planktonic larvae in the California Current. These are that any larvae referable to the Galatheidae (Gurney 1942), having a serrated rostrum in all except the first instar, not having an aciculate second antenna, and having a dorsal abdominal spine in later instars, can be considered to belong to *P. planipes*. In fact, this is by far the most abundant galatheid in the region, and galatheid larvae having the above characteristics far outnumber all other galatheid larvae.

The objects of this investigation were to identify the breeding areas and seasons of this important species, to determine the relative contributions of the adults in the benthic and pelagic phases to the larval population, and to determine to what extent the final ecdysis into the megalopa took place in water shallow enough to give

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[1] Present address: Fishery-Oceanography Center, Bureau of Commercial Fisheries, La Jolla, California 92037.

TABLE 1. *Breeding season of* Pleuroncodes planipes *from data on timing and composition of catches of larval forms in the CalCOFI plankton samples*

	Stage I larvae			Avg No./Sta. (individuals/m³ Sta.) Larval stages					
Date	Total Stas. (*N*)	Positive Stas. (%)	Max observed density (individuals/m³)	I	II	III	IV	V	Megalopas
1957									
Jan	57	10.5	5.6	0.12	0.14	0.19	0.03	–	0.01
Feb	60	25.0	151.6	4.84	3.07	0.77	0.45	0.01	–
Mar	84	25.0	63.9	2.04	0.90	0.83	1.32	0.31	0.09
Apr	126	19.8	13.3	0.46	1.01	0.01	0.33	0.36	0.21
May	82	3.7	0.5	0.01	0.10	0.02	0.01	0.01	0.04
Jun	114	–	–	–	–	0.01	0.01	0.01	0.05
Jul	182	–	–	–	–	–	–	–	0.02
Aug	14	–	–	–	–	0.01	–	0.01	–
Sep	14	–	–	–	–	–	–	–	–
Oct	46	–	–	–	–	–	–	–	0.01
Nov	–	–	–	–	–	–	–	–	–
Dec	–	–	–	–	–	–	–	–	–
1959									
Jan	129	24.0	7.6	0.22	0.39	0.01	0.01	–	0.01
Feb.	126	26.2	56.3	1.84	0.94	0.59	0.43	0.01	–
Mar	132	51.5	95.8	2.46	0.60	0.70	1.49	0.01	–
Apr	221	33.4	34.1	0.57	0.42	0.27	0.48	0.04	–
May	149	2.7	1.6	0.03	0.14	0.15	1.09	0.21	0.19
Jun	110	–	–	–	0.01	0.01	0.28	1.27	0.29
Jul	71	–	–	–	–	–	–	–	0.26
Aug	117	0.8	0.1	0.01	–	0.01	–	–	0.23
Sep	63	–	–	–	–	0.01	–	–	0.01
Oct	199	0.5	0.1	0.01	–	–	–	–	0.01
Nov	38	10.5	0.1	0.01	–	–	–	–	–
Dec	45	13.3	0.5	0.04	–	–	–	–	–
1960									
Jan	248	33.0	97.2	1.65	0.11	–	–	–	–
Feb	163	50.3	171.9	2.63	0.01	–	–	0.01	–

the megalopas the possibility of entering the benthic phase without drifting into the oceanic environment. The material comprised 2,546 plankton samples taken during the CalCOFI[2] cruises with a standard 1-m net fished in a standard fashion to a depth of 140 m (Ahlstrom 1948); such samples are available from a 15-year period, but 1957 and 1959 were selected for their good coverage and because the first was a typical cool year, the second a warm year (Sette and Isaacs 1960). The coverage was later extended a few months into 1958 and 1960. Aliquots of the total samples were examined, and 483 of these were found to contain zoeae or megalopas of *P. planipes.* Also available were the data on the occurrence of adults of the pelagic phase of the same species in the same plankton hauls, which had already been discussed in relation to the changing hydrographic conditions of this period (Longhurst 1967*a*).

I am extremely grateful to D. L. R. Seibert who was responsible for the acquisition of data, and who performed most of the examinations of the plankton samples himself. The work was supported by the Bureau of Commercial Fisheries under contracts 14-17-007-139/221 and formed part of the Scripps Tuna Oceanography Research Program.

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[2] California Cooperative Oceanic Fisheries Investigations.

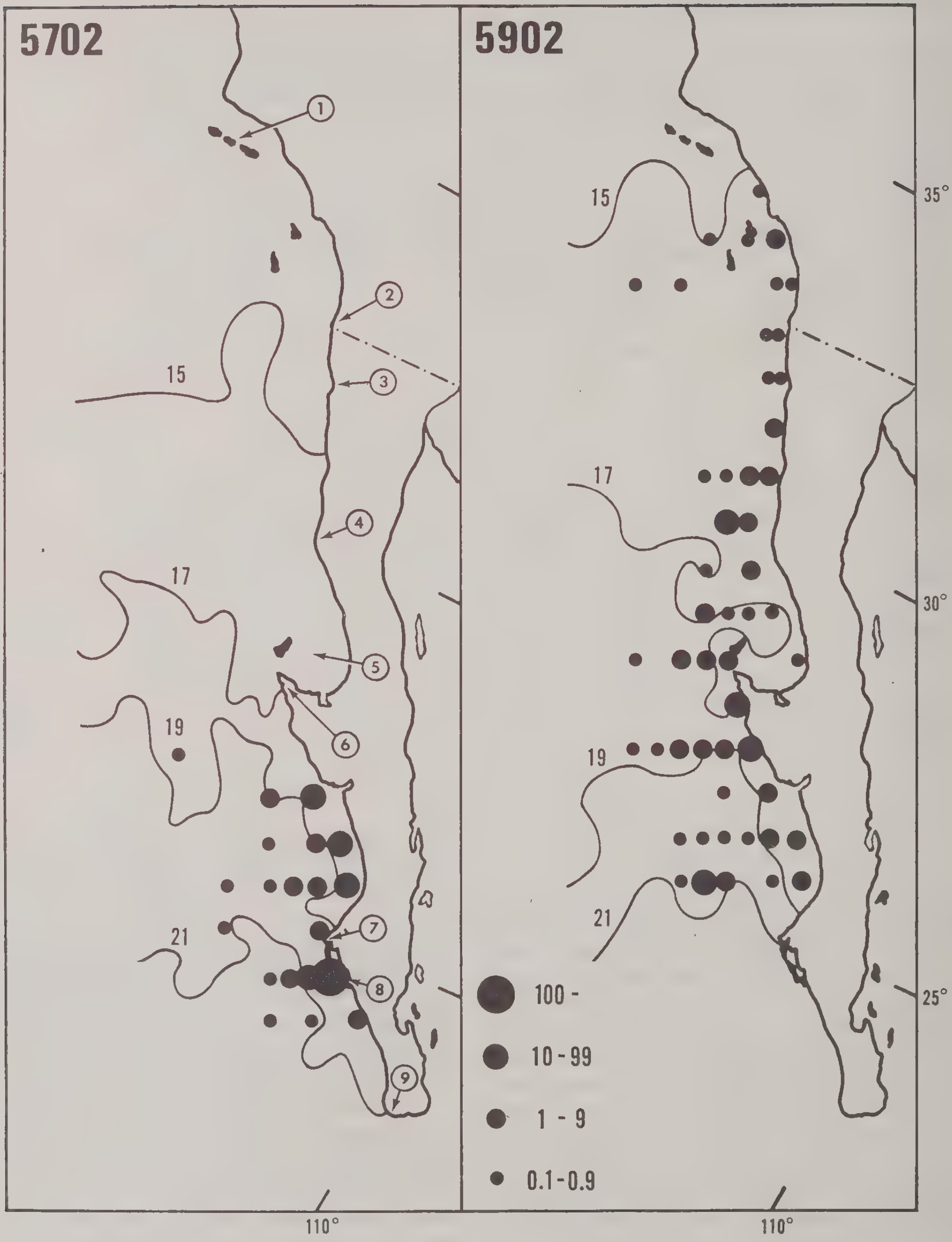
TABLE 2. *Frequency distribution of temperatures at 10 m at stations where* Pleuroncodes planipes *larvae occurred in the plankton samples*

	Temp (°C)																	
	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11
1957																		
Jan	–	–	–	–	–	–	–	1	6	1	1	–	–	–	–	–	–	–
Feb	–	–	–	–	–	–	3	3	4	11	6	1	1	–	–	–	–	–
Mar	–	–	–	–	–	–	–	–	1	5	9	3	3	3	–	1	–	–
Apr	–	–	–	–	–	–	2	8	3	2	10	2	3	7	1	2	–	–
May	–	–	–	–	–	–	–	–	–	1	2	–	8	6	1	–	–	–
Jun	–	–	–	–	–	–	7	1	1	5	4	6	1	–	–	–	–	–
Jul	–	–	–	–	–	–	7	1	1	1	–	–	–	–	–	–	–	–
Aug	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
Sep	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oct	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
Nov	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dec	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1959																		
Jan	–	–	–	–	–	2	8	11	3	5	6	2	5	4	–	–	–	–
Feb	–	–	–	–	–	–	–	1	3	2	9	7	10	15	21	1	–	–
Mar	–	–	–	–	–	–	–	–	2	3	8	9	17	13	5	3	–	–
Apr	–	–	–	–	–	–	–	–	6	11	7	9	24	20	15	5	1	2
May	–	–	–	–	–	–	–	–	–	–	–	9	15	8	2	5	1	2
Jun	–	–	–	–	–	–	–	–	–	–	8	6	16	5	–	–	–	–
Jul	–	–	–	–	–	–	3	5	15	5	4	2	1	1	–	–	–	–
Aug	1	–	2	5	5	4	1	1	1	2	2	1	1	–	–	–	–	–
Sep	–	–	–	–	–	1	1	–	–	–	–	2	–	–	–	–	–	–
Oct	–	–	–	1	1	–	1	1	–	–	–	–	–	–	–	–	–	–
Nov	–	–	–	–	–	–	–	–	–	–	–	2	1	1	–	–	–	–
Dec	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TEMPORAL AND SPATIAL DISTRIBUTION OF BREEDING

Boyd and Johnson (1963) examined adult *P. planipes* taken in the CalCOFI net tows during 1959 and 1960 and found that ovigerous females occurred only from December to the end of March and comprised more than 50% of all females taken during February; these data support their observation, but indicate that stage I larvae (which are unlikely to have been released from the females more than 10 days earlier) occur in the samples for more than the four months in which ovigerous females were taken (Table 1). In 1957, stage I larvae were taken until the end of May, though peak abundance was in February; the same pattern was seen during 1959, although in that year the peak occurred during the March cruise. In the breeding season of 1959–1960, which was covered in its earlier stages better than during other years, breeding apparently began in late summer and occurred rather commonly during October, November, and December. There is a general correspondence between the level of maximum abundance in any sample and the number of stations with larvae in the same month, so that breeding is most widespread when it is most intense in any region.

The timing of breeding was remarkably little altered during the warm year 1959–1960 compared with the more usual conditions during early 1957. Since the net tows from which the samples were obtained integrated the plankton of the upper 140 m, there is no information available on the distribution of the larvae with depth, but they are presumed to have occurred mostly in the mixed layer. Thus, it may be valid to compare their distribu-


5702
5902
①
②
③
④
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⑥
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⑧
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15
17
19
21
35°
30°
25°
110°
110°
100 -
10 - 99
1 - 9
0.1 - 0.9

FIG. 1. Distribution of stage I larvae in February 1957 and February 1959 and of the 10-m isotherms in the same months, showing that the northward shift of *Pleuroncodes* was greater than the northward shift of the isotherms. The units are numbers of individuals per m^3 of water filtered. Geographical locations indicated by numbers, thus: 1—Channel Islands; 2—San Diego; 3—Ensenada; 4—Cape Colnett; 5—Sebastian Vizcaino Bay; 6—Point Eugenia; 7—Point San Lazaro; 8—Magdalena Bay; 9—Cape San Lucas.

tion in the samples with the distribution of temperatures at a depth of 10 m. The data in Table 2 indicate that there were considerable differences in these temperatures at stations at which larvae occurred between the two years, notably in the months of January and February when a high percentage were in stages I or II. There is evidence that breeding occurred in colder water in 1959 than in 1957—quite contrary to expectation. Fig. 1 shows that in February 1959, as compared with February 1957, there had been a shift of both breeding adults (indicated by larvae) and surface isotherms towards the north; it also shows that the crabs were displaced farther northwards in 1959 than were the isotherms.

As the breeding season advanced in each of the two years, the early larvae occurred in progressively cooler water until about May when temperatures began to rise and progressively later larval stages predominated in the catches. Examination of the monthly plots of larval distribution in the samples shows that in the first four or five months of the year not only does breeding occur progressively farther towards the north (especially in 1959), but also the inshore regions along the coasts of southern and Baja California become more influenced by the effects of coastal upwelling, so that inshore temperatures drop. Later in the year when older zoeae and megalopas were found in water with temperatures in excess of 25C, upwelling had ceased (Reid, Roden, and Wyllie 1959) and larval populations were far offshore. The range of temperatures at which early zoeae were found corresponds rather closely to the range of tolerance established experimentally by Boyd and Johnson (1963) for *Pleuroncodes* larvae. Only in the later stages, and particularly as megalopas, were larvae found at temperatures in excess of 20C (above which Boyd and Johnson were not able to culture larvae through their complete development).

Early larvae (stages I and II) were present over a rather extended area off southern and Baja California in months in which breeding occurred, but there were typically several rather restricted areas where larvae were present in numbers higher than over the wider area by a factor of 10 or even of 100. Such areas have been supposed to represent major concentrations of the adult breeding populations.

In 1957 these areas were found only on the coast of Baja California and only over the continental shelf; during January a patch of early larvae appeared that was close to the coast in the bight south of the Point Eugenia peninsula, and in the following month much of this bight was occupied by the larvae (stage I and II combined reached a maximum density of $130/m^3$). Farther to the south, over the shelf close in to Cape San Lazaro and Santa Margarita Island, a breeding concentration occurred in the first four months of the year; early larvae reached a maximum density of $189/m^3$ in February just off the edge of the shelf at Santa Margarita Island (Sta. 143.45).

In 1959 the breeding concentrations extended along the coast of southern California as far north as Point Conception. In January and February, breeding occurred along the northern coast of the Santa Barbara Channel, but densities of early larvae as low as $2/m^3$ were encountered in this region; in March, there was a dense concentration of stage I and II larvae in Sebastian Vizcaino Bay that reached a maximum density of $97/m^3$ at Sta. 120.25. To the south of the Point Eugenia peninsula a high concentration occurred during February and March and occupied much of the bight between there and Cape San Lazaro in a position similar to the 1957 high concentration. In March a density of $61/m^3$ was recorded.

These patches of larvae could have originated either from the stocks of benthic adult *P. planipes* known, in general terms, to occur on the upper part of the continental slope along the coast of Baja California in cool years (Boyd 1963, 1967; Longhurst 1967*a*, *b*), or they could have originated from pelagic stocks in the same area. The distribution of adults of the pelagic phase was examined to determine

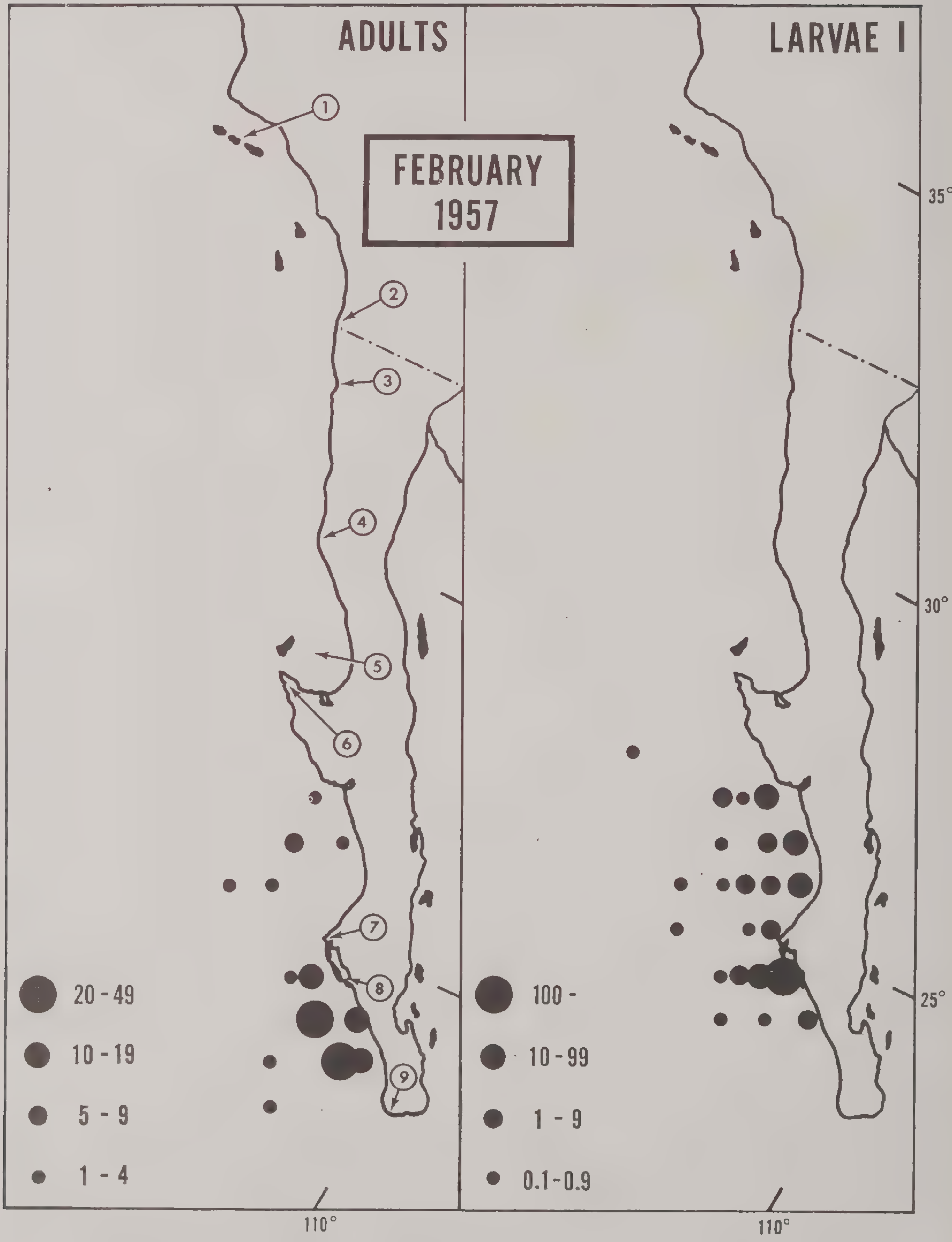
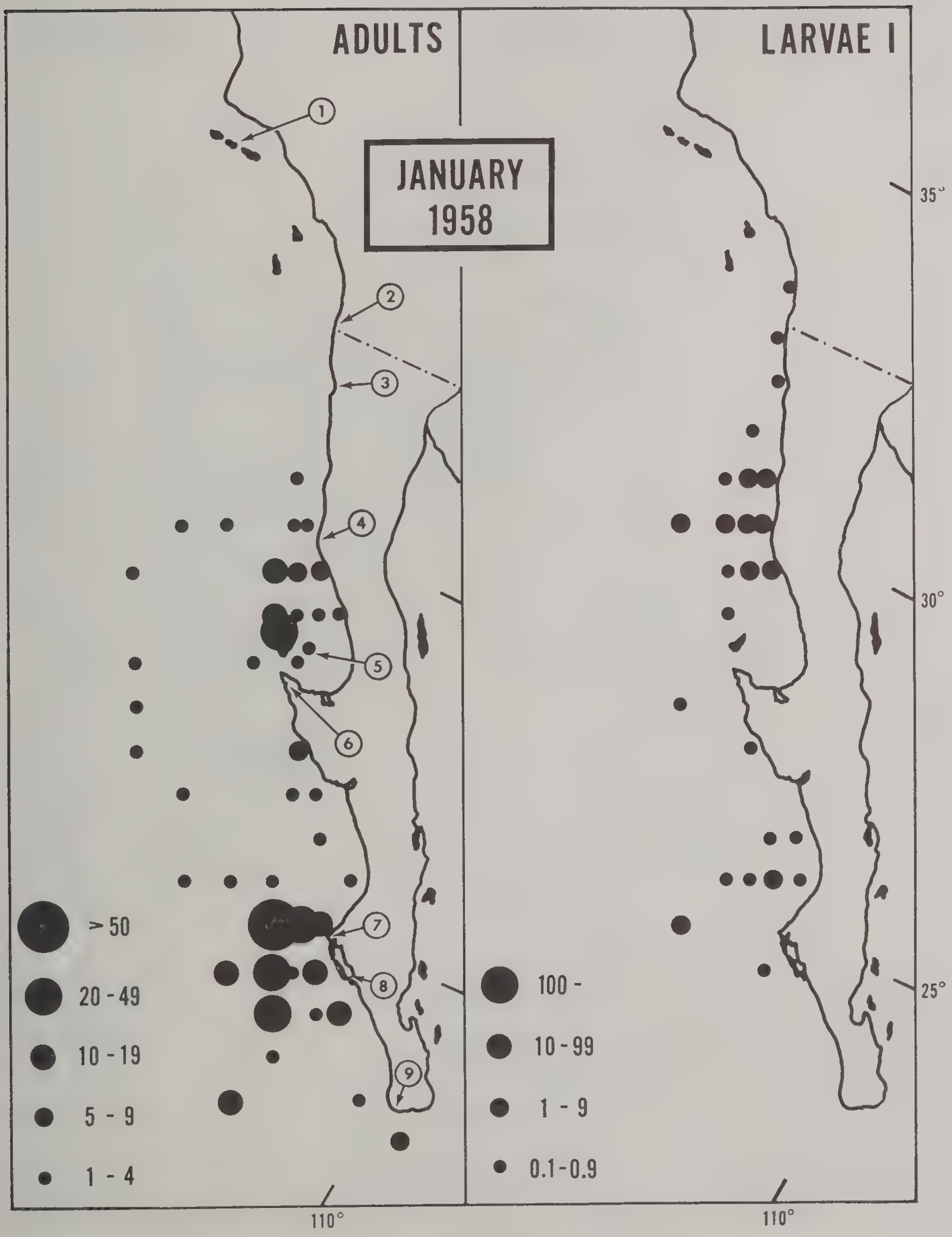

ADULTS
LARVAE I
FEBRUARY 1957
1
2
3
4
5
6
7
8
9
35°
30°
25°
110°
110°
20 - 49
10 - 19
5 - 9
1 - 4
100 -
10 - 99
1 - 9
0.1-0.9

FIG. 2. Distribution of adult and of stage I *Pleuroncodes* in the CalCOFI plankton samples February 1957. Units: adults as number per standard haul; larvae as number per m^3.


ADULTS
LARVAE I
JANUARY
1958
①
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③
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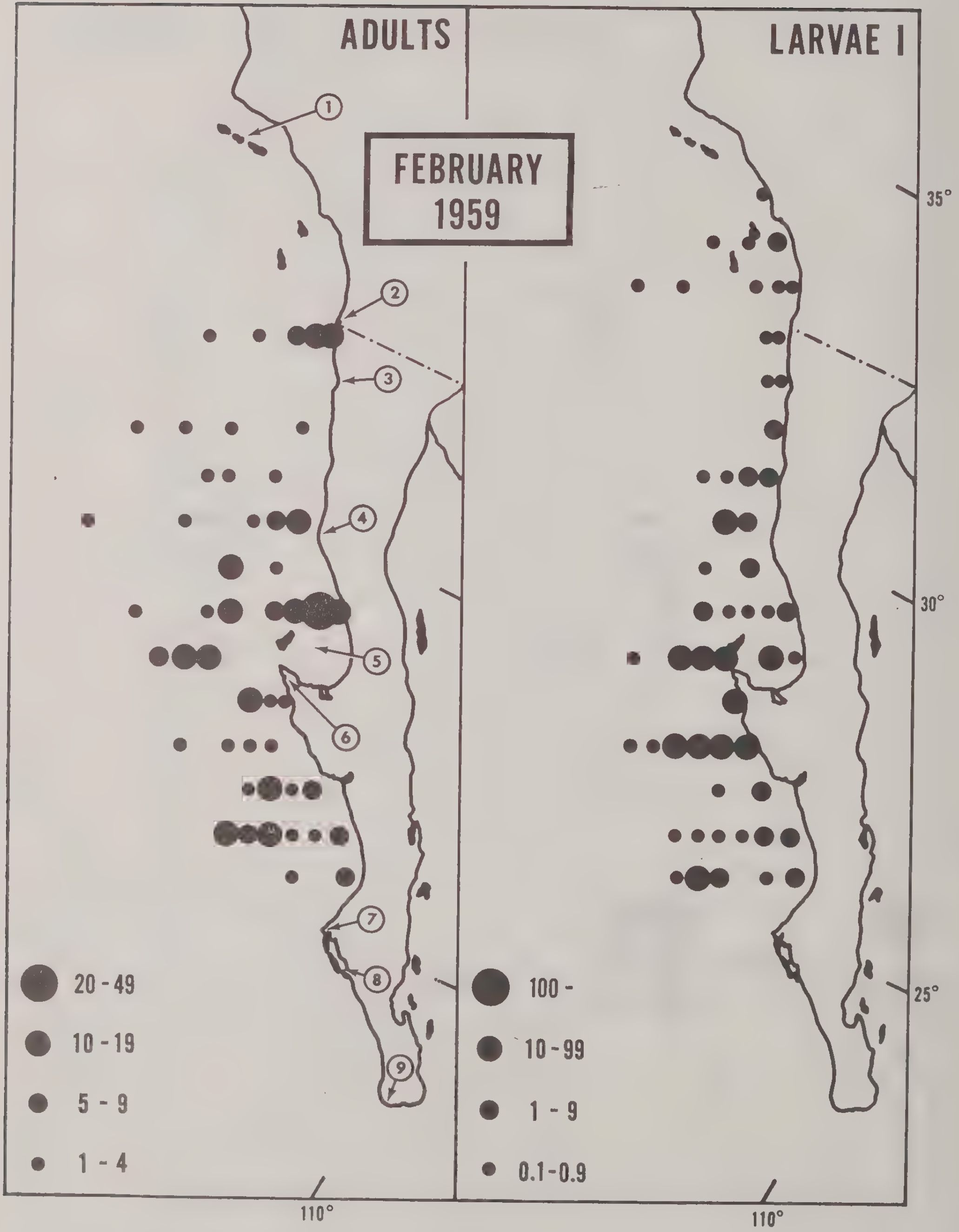
⑤
⑥
⑦
⑧
⑨
35°
30°
25°
110°
110°
> 50
20 - 49
10 - 19
5 - 9
1 - 4
100 -
10 - 99
1 - 9
0.1-0.9

FIG. 3. Distribution of adult and of stage I *Pleuroncodes* in CalCOFI plankton samples in January 1958. Units and locations as Figs. 1 and 2.


ADULTS
LARVAE I
FEBRUARY
1959
①
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④
⑤
⑥
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⑧
⑨
35°
30°
25°
110°
110°
● 20 - 49
● 10 - 19
● 5 - 9
● 1 - 4
● 100 -
● 10 - 99
● 1 - 9
● 0.1-0.9

Fig. 4. Distribution of adult and of stage I *Pleuroncodes* in the CalCOFI plankton samples in February 1959. Units and locations as Figs. 1 and 2.

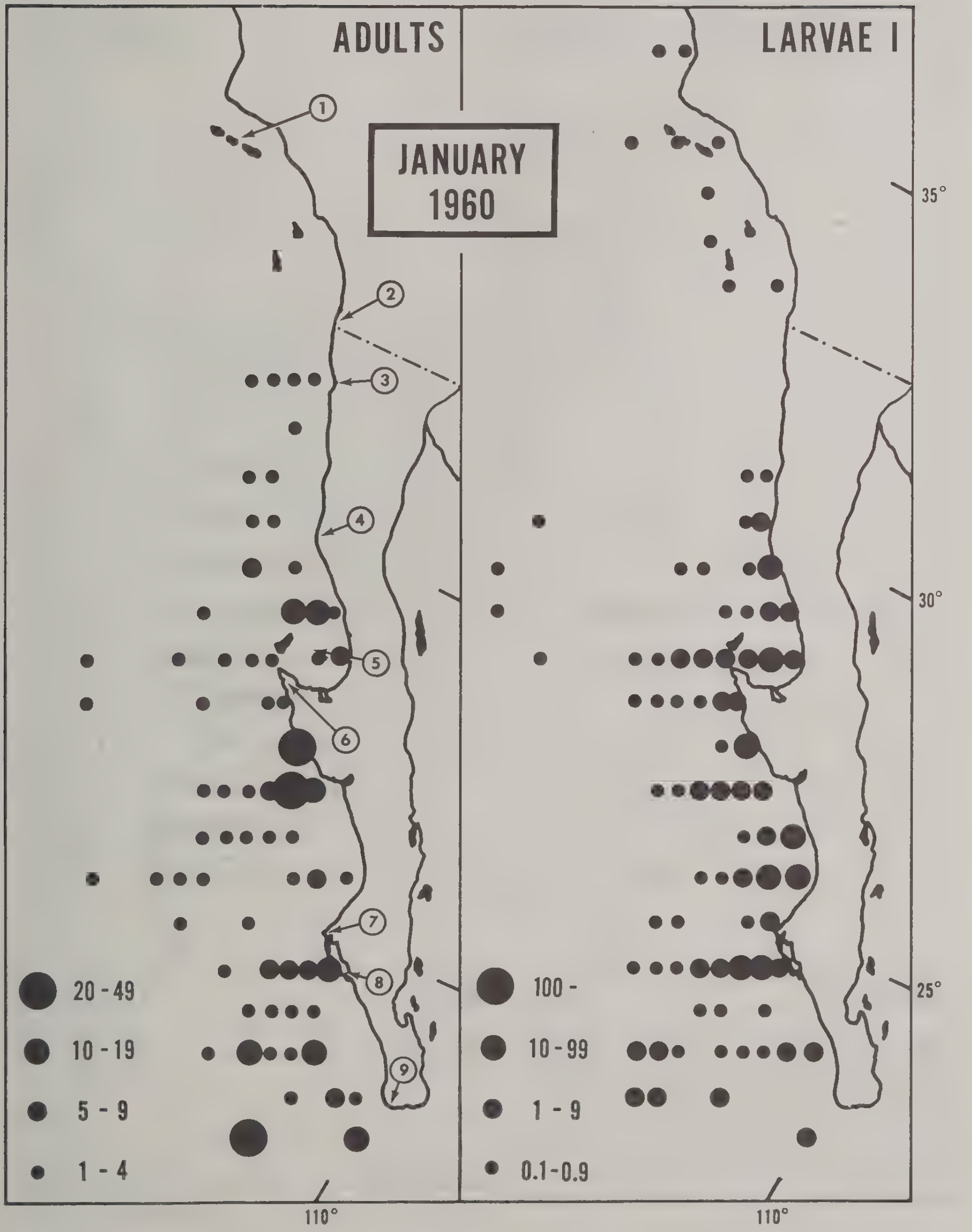
ADULTS
LARVAE I
JANUARY
1960
①
②
③
④
⑤
⑥
⑦
⑧
⑨
35°
30°
25°
110°
110°
20 - 49
10 - 19
5 - 9
1 - 4
100 -
10 - 99
1 - 9
0.1-0.9

FIG. 5. Distribution of adult and of stage I *Pleuroncodes* in the CalCOFI plankton samples in January 1960. Units and locations as Figs. 1 and 2.

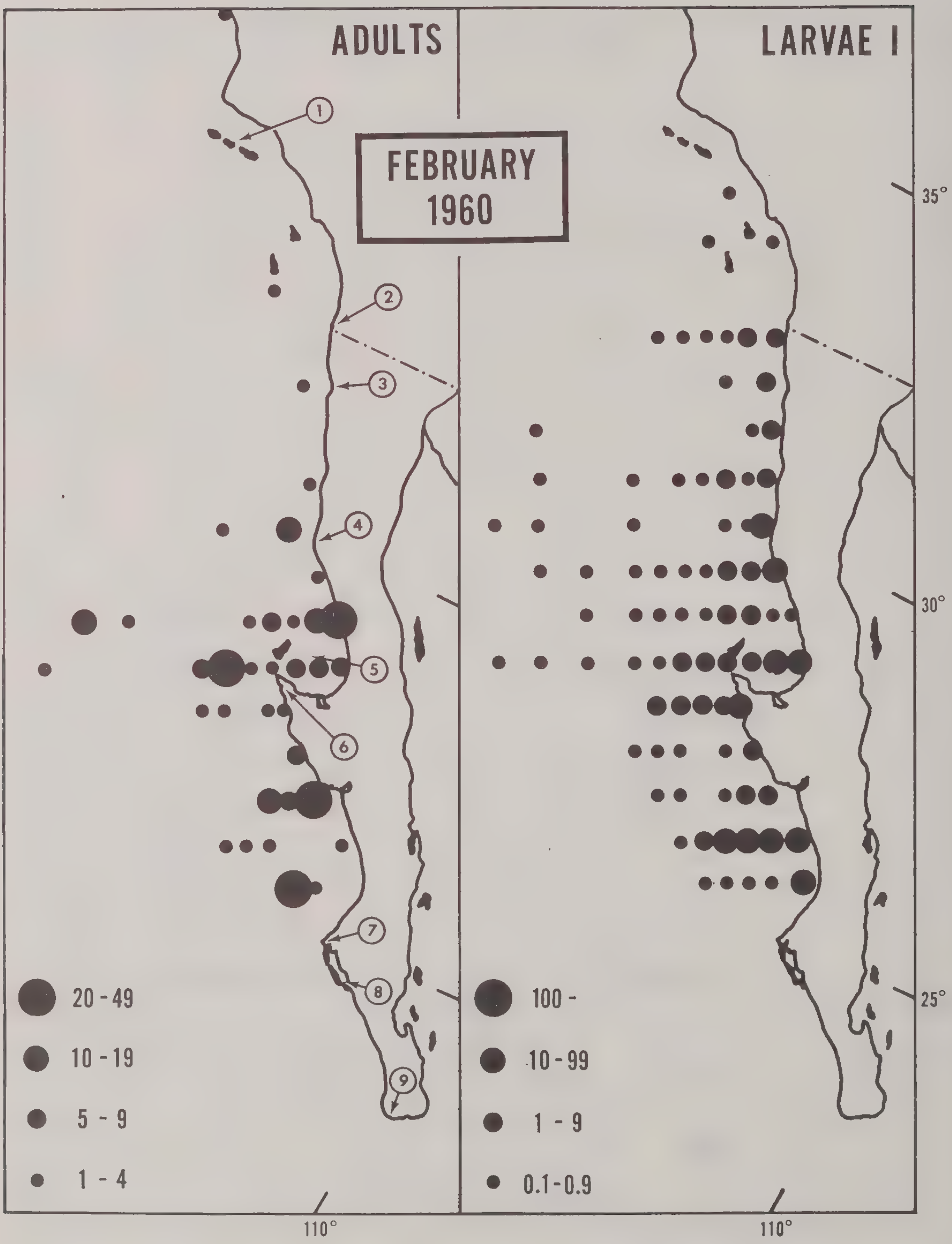
ADULTS
LARVAE I
FEBRUARY
1960
1
2
3
4
5
6
7
8
9
35°
30°
25°
110°
110°
20 - 49
10 - 19
5 - 9
1 - 4
100 -
10 - 99
1 - 9
0.1 - 0.9

FIG. 6. Distribution of adult and of stage I *Pleuroncodes* in the CalCOFI plankton samples in February 1960. Units and locations as Figs. 1 and 2.

if such stocks were present in the required areas in these two years at the periods of peak spawning: The evidence was conflicting.

In February 1957 (Fig. 2), the general occurrence in the region of Baja California of pelagic adults and stage I larvae corresponded, but the detailed distribution showed many anomalies. In particular, the highest numbers of each occurred at different locations. At Sta. 143.25 off Santa Margarita Island there were 151 larvae/m^3, but no adults; these were most abundant between 80 and 130 km to the southwest at Stas. 147.30 and 150.25. It is supposed, therefore, that this patch of larvae had an origin in benthic rather than pelagic phase adults.

In January 1958 (Fig. 3), pelagic adults extended farther offshore and to the southwest than the larvae, while these extended farther north along the coast than the pelagic adults. There was good evidence to the west of Cape San Lazaro of a larval patch derived from pelagic adults, as is evident in the figure. The same is seen, but less clearly, to the west and northwest of Cape Colnett.

In February 1959 (Fig. 4), the correlation between adults and early larvae was not clear, for larvae were distributed rather evenly along the whole surveyed coastline with unusually low variation in larval densities between regions; however, in each case where larvae were observed away from the coast, they were in relatively close proximity to collections of pelagic adults.

Finally, in 1960 (Figs. 5 and 6) the same pattern is seen again; there are offshore patches of stage I larvae, much too far from the coast to have drifted off during the first instar, which correspond with patches of pelagic adults. There are also inshore patches, again predominantly on the Baja California coast, where large numbers of larvae occur with few or no adults, and which seem to indicate breeding by the benthic stocks. As in the two previous years, both warm seasons, the larvae occurring sparsely along the coast of southern California do not appear to be correlated with the presence of pelagic adults. The correspondence between the distribution of offshore adults and larvae, where neither are present in high concentrations, cannot be expected to be precise: A zooplankton net is a far more efficient sampler of larvae (having relatively large numbers per unit volume and little avoidance ability) than of adults (relatively sparse and relatively efficient avoiders of nets). It is assumed that samples of offshore larvae, in rather low concentrations and apparently in the absence of adults, were actually the result of spawning by nearby pelagic adults that were missed by the sampling technique used.

The evidence can be summarized thus: offshore concentrations of early larvae always appear to be correlated with the presence of pelagic adults, while the converse is not necessarily true—even during the breeding season there are patches of adults offshore unaccompanied by larvae. The greatest concentrations of early larvae are always, notwithstanding the above statement, over or close to the continental shelf and frequently in areas where few or no pelagic crabs accompany them in the samples.

Apparently, the pelagic adults that were swept northwards along the coast of southern California from late 1957 to mid-1959 by the unusual conditions of flow in the California Current in this period (Boyd 1967; Glynn 1961; Longhurst 1967*a*) were able to breed in regions far to the north of their usual breeding range.

SUBSEQUENT HISTORY OF LARVAL PATCHES

The duration of the larval stages varies considerably (Boyd and Johnson 1963); stage IV, comprising from four to eight instars, occupies about 50–60% of the total duration of larval development, while the other stages comprise only a single instar. This is reflected in the total catch composition of larvae in a year's samples, expressed in per cent:

Year	I	II	III	IV	V	Megalopa
1957	44.5	31.5	9.1	10.7	3.3	1.5
1959	25.9	15.9	9.5	28.6	13.6	6.3

It would be unrealistic to use these figures to make estimates of mortality rates, because it is not known whether all stages involved were equally well sampled. There are reasons to suspect that they were not: early larval patches are small and dense, later larvae are more widespread; older larvae undoubtedly avoid nets better than early stages; there may well be a differential in the relative depth distribution of early and late stages. That the percentage catch composition follows approximately the pattern expected from the known relative duration of each stage (Boyd and Johnson 1963) indicates that no gross sampling differential occurred and that for relative distribution purposes the data are probably adequate.

Larvae of *P. planipes* occur in a general area of overall offshore drift of water from the coast away to the southwest as the California Current turns in this direction. Johnson (1960) has discussed this in relation to the coastal spiny lobster *Panulirus interruptus*; the situation poses certain problems for the retention of enough larvae during a long larval life so that a sufficient number can finally settle onto the continental shelf after metamorphosis. There is usually a large population of late megalopas and small subadult *P. planipes* in the southwest corner of the CalCOFI station pattern in late summer. This population stretches at least 320 km to the southwest of Cape San Lucas and oceanic populations comprised mostly small subadult individuals occur up to 1,600 km offshore (Longhurst 1967*a*).

The data were examined for evidence of the offshore movement of late larvae and megalopas or of the direct settlement of megalopas into the benthic phase without a prior offshore advection. The subsequent history of the larval patches representing major centers of breeding were traced up to six months, with the following results.

The February 1967 patch in the bight south of Point Eugenia was traced to a patch of stage III and IV larvae in the central bight in March and to stage V larvae and megalopas at the continental edge in the same area in April; in June a patch of megalopas was found at Sta. 130.60 and again in July at 130.70 about 130 km beyond the edge of the continental shelf. The geostrophic flow pattern for July (Wyllie 1966) shows complex offshore eddies in this region capable of producing the observed offshore transport.

The patch observed in January 1957 south of Cape San Lazaro grew in size and in density of early larvae until April, and during this time changes in the relative distribution of the various stages were observed. The following were numbers per m^3 of the early larval stages observed at Sta. 143.35 just clear of the shelf off Santa Margarita Island:

1957	I	II	III
Feb	152	28	1
Mar	64	37	25
Apr	13	2	1

In March there were also 29 stage IV/m^3 at this coastal station, but by April the concentration of later larvae had moved to the southwest; at Sta. 150.45 about 190 km from the coast there were 17 stage IV, 33 stage V, and 10 megalopas per m^3. There was no cruise in May, and by June a patch of megalopas at Sta. 153.40 (another 65 km southwards) represented the remnants of the original breeding patch. This movement is in general agreement with the observed geostrophic flow.

In 1959 the larval patch that developed in the region of the Santa Barbara Channel in January and February gave rise to a patch of stage IV larvae in March outside the Channel Islands and stage V larvae in the same area in April. No megalopas were seen in this region, and the patch was not traced any further.

The breeding that occurred in Sebastian Vizcaino Bay in March 1959 was not traced beyond the initial month; before the cruise in April, the bay was flushed clear of larvae. Their fate could not be traced because of the large larval patches of local origin south of Point Eugenia with which they are presumed to have mingled.

The patch originating in February 1959 south of Point Eugenia could be traced more satisfactorily. In accordance with a general southerly and uneddied flow of the California Current, this patch had moved southwards by March and contained stage IV larvae up to 93/m^3; it had reached the center of the bight between Point Eugenia and Cape San Lazaro by April, maintaining about the same composition. In May, there was derived from this a rather complex offshore distribution of patches comprising stages IV and V (predominantly the latter) and postlarvae to a density of 15 megalopas/m^3. This situation remained similar in June and July when there was an indication of offshore geostrophic flow from the bight, and megalopas were centered at Sta. 137.45 about 110 km west of Cape San Lazaro. Finally, in July the geostrophic flow in this region indicated that an anticyclonic eddy gave a northwest transport, which was in fact confirmed by the distribution of megalopas that were now concentrated about 225 km southwest of Point Eugenia.

There is, thus, sufficient evidence to demonstrate the offshore transport of late larvae and of megalopas having their origin in coastal breeding centers. It is clear that at least a significant percentage of these larvae have this fate if the normal processes of mortality allow them to reach the megalopa stage; it is also clear from such data as those for 1957, when the megalopas were last detected far to the west of Cape San Lucas, that this transport is sometimes continued into oceanic regions with no likelihood of immediate return to the region of the coast by eddying. The question of whether any megalopas achieve the benthic phase directly over the continental shelf has hardly been resolved by these data. To settle this question, a search for small subadults should be directed to the deeper parts of the shelf south of Point Eugenia and to the south of Santa Margarita Island in the months of May and June.

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THE BIOLOGY OF MASS OCCURRENCES OF GALATHEID CRUSTACEANS AND THEIR UTILIZATION AS A FISHERIES RESOURCE

by

A.R. LONGHURST
Bureau of Commercial Fisheries
Fishery-Oceanography Center
La Jolla, California, U.S.A.

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Abstract

Five known species of Galatheidae exhibit the phenomenon of mass occurrences, mostly in highly eutrophic regions of the ocean. Two of the species (Munida gregaria and Pleuroncodes planipes) occur in vast pelagic swarms as juveniles or young adults, and both species have the capacity to graze on diatom blooms. These two species and M. subrugosa, Cervimunida johni and P. monodon occur in benthic concentrations on some parts of the continental shelf, often in water of very low oxygen tension. A fishery off Chile for the last two of these species lands 10×10^3 metric tons yearly, and it is postulated that the unexploited populations of Pleuroncodes planipes could produce similar or greater yields. It is probable that a demersal fishery for this species will shortly be developed, and it is possible that the fishery may include exploitation of the pelagic phase, though this seems less practicable. It is tentatively postulated that the five species of galatheids reviewed may have a total annual potential of between 30×10^3 and 300×10^3 tons, under the same type of exploitation as has developed in the Chilean fishery.

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LES APPARITIONS MASSIVES DE GALATHEES : BIOLOGIE ET UTILISATION COMME RESSOURCE HALIEUTIQUE

Résumé

Cinq espèces connues de Galatheidae se concentrent en essaims massifs, principalement dans les régions fortement eutrophiques de l'océan. Deux d'entre elles *Munida gregaria* et *Pleuroncodes planipes*, forment de grands rassemblements pélagiques aux stades juvénile ou jeune adulte, et toutes deux peuvent brouter les bancs de Diatomées. Ces deux espèces, ainsi que *M. subrugosa*, *Cervimunida johni* et *P. monodon*, se trouvent en concentrations benthiques en certains points du plateau continental, souvent dans les eaux à très faible tension d'oxygène. Au large du Chili, la pêche des deux dernières espèces mentionnées produit annuellement 10 x 10^3 tonnes, et l'on suppose que les populations inexploitées de *Pleuroncodes planipes* pourraient fournir un rendement analogue ou supérieur. Il est probable que l'on entreprendra sous peu la pêche démersale de cette espèce, et il se peut que l'on s'efforce d'exploiter aussi la phase pélagique, bien que ceci paraisse moins faisable. On attribue provisoirement aux cinq espèces de Galathées examinées un potentiel annuel global situé entre 30 x 10^3 et 300 x 10^3 tonnes, pour un type d'exploitation analogue à celui de la pêcherie chilienne mentionnée plus haut.

LA BIOLOGIA DE LA PRESENCIA EN GRANDES CANTIDADES DE CRUSTACEOS GALATEIDOS Y SU APROVECHAMIENTO COMO RECURSO PESQUERO

Extracto

Existen grandes masas de cinco especies conocidas de Galatheidae sobre todo en las regiones altamente eutróficas del océano. Dos de ellas (*Munida gregaria* y *Pleuroncodes planipes*) aparecen en vastos enjambres pelágicos de individuos juveniles o adultos jóvenes, y ambas especies se alimentan en las floraciones de diatomas. Estas dos especies y *M. subrugosa*, *Cervimunida johni* y *P. monodon* aparecen en concentraciones bénticas en algunas partes de la plataforma continental, frecuentemente en aguas de muy baja tensión de oxígeno. Una pesquería frente a las costas chilenas desembarca de estas dos últimas especies 10 x 10^3 toneladas métricas anuales, y se supone que las poblaciones sin explotar de *Pleuroncodes planipes* podrían producir un rendimiento parecido o mayor. Es probable que pueda crearse en breve una pesquería demersal de esta especie, aunque esto parece menos practicable. En principio se supone que las cinco especies de galateidos examinadas pueden tener un potencial total al año entre 30 x 10^3 y 300 x 10^3 toneladas, con arreglo al mismo tipo de explotación que se ha establecido en la pesquería chilena.

1 INTRODUCTION

The Galatheidae are a family of generalized Crustacea Anomura which occur widely, from tropical seas to high latitudes and from the littoral zone down to abyssal depths, generally as members of benthic species assemblages. It appears that at least five of the species which live on the continental shelf can occur in great concentrations at certain times and places within their geographical ranges, and it is these mass occurrences which appear to have fishery potential and which are the subject of this review. Other species in other parts of the oceans may also exhibit the same phenomenon, but have escaped the notice of the reviewer.

In talking of these crustaceans to the fishing industry, one is faced with the problem of their nomenclature in the vernacular; they are neither shrimps nor prawns in the English sense, though they may be utilized by the shrimp industry, nor are they crabs, though the name is often applied to them by fishermen. Having no true vernacular name in any language, fishermen and biologists have applied to them epithets derived from other crustacea, unrelated but of approximately similar appearance: thus the 'red crabs' of the American tuna fishermen, the 'langostino' of the Chilean shrimp fishermen. There is no simple solution to such a problem, except that of being aware of its existence and of taking care to check independently what species or genera are involved.

The five species which are known to show mass occurrences are tabulated below and grouped geographically. It will be noted that all these species have ranges within relatively eutrophic areas of the ocean, in which strong phytoplankton blooms are a seasonal occurrence.

(i) Munida subrugosa (White), Munida gregaria (Fabricius): 'whale-feed', 'lobster-krill'; New Zealand, Tasmania, Sub-Antarctic islands, Patagonia.

(ii) Cervimunida johni Porter: 'langostino azul', 'langostino amarillo'; Pleuroncodes monodon (H. Milne Edwards): 'langostino colorado', 'zanahoria'; Humboldt Current.

(iii) Pleuroncodes planipes Stimpson: 'red crab', 'pelagic crab'; California Current, Gulf of California.

These species appear to share some biological characteristics which may have some significance in the mass occurrences: (i) Each species shows a wide range of feeding mechanisms, often including the capability of grazing, by filtration, upon blooms of the larger phytoplankton organisms. (ii) The life-history includes a postlarval pelagic phase, which may be rather ephemeral, may be repeated later in the life of an individual, or may extend at least until first maturity. (iii) The mass occurrences of adults in the benthic phase tend to occur both in locations below mass diatom blooms and at depths corresponding to those at which oxygen deficient water meets the continental slope.

The paper examines these factors in relation to the distribution and present and future exploitation of the species.

2 SUB-ANTARCTIC RESOURCES

2.1 Biology

The most complete account of the biology of M. subrugosa and M. gregaria is that of Matthews (1932), who shows clearly that these two similar species are in fact distinct, though their geographical ranges very largely coincide. The most important difference between the two species is that M. gregaria is very commonly found in the pelagic as well as the benthic phase, while M. subrugosa has no prolonged pelagic phase after larval development is completed. The following account of these two species is drawn very largely from that of Matthews, based on material from the South Atlantic. Pelagic M. gregaria from off New Zealand have been examined and found to conform exactly to his descriptions of morphology and stomach contents.

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The pelagic phase of M. gregaria is morphologically distinct from the benthic phase, and was described as a separate genus (Grimothea Leach). The principal distinction, apart from a usually lighter and less spinous exoskeleton, is the great development of the third maxillipeds as flattened, foliaceous, filtering appendages in the pelagic phase. In the benthic phase, these limbs remain foliaceous but are relatively much reduced. The young M. subrugosa, on the other hand, closely resemble the adult in all but size from the time of completion of larval development.

The place occupied in the life history of M. gregaria by the pelagic phase (or grimothea stage) has not directly been investigated, but it appears to be of variable duration. Chilton (1909), working on records of the New Zealand population, and Matthews (1932), considering the Patagonian records, were of the opinion that the point in the life history at which settlement occurred was labile and depended upon the circumstances facing the stock of young pelagic individuals. If conditions for settlement into the benthic phase were not suitable (because they found themselves over oceanic depths, for example), they could prolong the pelagic phase, while other stocks would settle early in their lives. It appears possible for the pelagic phase to be extended at least until the time of first maturity, and ovigerous grimothea stages have been recorded for this species. Thus, while the normal pelagic individuals have carapace lengths within the range 7 to 12 mm, and benthic adults 20 to 38 mm, individuals in the grimothea stage may be larger than the smaller benthic adults.

Evidence is given later that an alternation between the pelagic and benthic phases can occur during the life of an individual, but this is apparently not a regular occurrence.

It has been shown that the stomach contents of the pelagic phase frequently comprise masses of partially digested diatoms (Kemp, in Matthews, 1932), and this was confirmed by examination of specimens in the plankton collections of the Scripps Institution of Oceanography. As shown below for Pleuroncodes planipes, it is the function of the third maxillipeds to act as a filtering mechanism when grazing on phytoplankton blooms. On the whole the species is a very catholic feeder, and in the benthic phase it eats small organisms captured by the chelipeds and organic detritus from the upper deposit levels.

2.2 Range of pelagic phase

Matthews (1932) documents many accounts from early voyagers of the mass occurrences of the pelagic phase of Munida gregaria, beginning with that of Sir Richard Hawkins in 1594 who named 'Crabby Cove' in the Straits of Magellan after the fact that the water was 'full of a small kind of red crabbes'. It is evident from these accounts by Dampier, Banks and other early voyagers, together with the modern accounts from, for example, the METEOR and DISCOVERY expeditions, that mass surface occurrences of the grimothea stage are commonplace, especially in the early summer. They are reported from both coasts of Patagonia, to 41°S on the west, and to 51°S on the east, around the Falkland Islands, the coasts of New Zealand and its sub-Antarctic islands, and the coast of Tasmania. Although it is not possible to quantify these accounts, the repetition within them of statements as to the occurrence of 'clouds' of little red lobsters at the surface, of the sea being coloured red with small galatheids, and so on, leaves little doubt as to the magnitude and concentration of the populations.

It is also evident from the published records that these mass occurrences may occur either close to land, over the continental shelf, or over oceanic depths at some hundreds of miles from land. The factors inducing settlement are obscure, but probably are connected with the nutrient cycle of the sea area concerned and the chance of pelagic stocks being carried by horizontal advection off the continental shelf.

There are a few records of adult M. gregaria being taken at the surface, especially along the western coast of Patagonia. These individuals in the DISCOVERY collections do not have grimotheal characters, yet were dip-netted at the surface from enormous concentrations extending from 45°S to 50°S. At the same latitude there are records of windrows of these galatheids being drifted ashore in very great numbers.

2.3 Range of benthic phase

Records of mass benthic occurrences of these two species are less common, perhaps simply because they are not exposed to the view of the curious voyager; nevertheless, there are published records which indicate that they occur. Thompson (1898) records massive summer occurrences of benthic individuals of M. subrugosa in Otago Harbour, New Zealand, and the DISCOVERY collections include adult M. gregaria, trawled in abundance in 25 to 115 m of water off East Falkland Island. Cooked in the ship's galley, these were found to be of very good flavour (Matthews, 1932).

2.4 Exploitation

Neither of these two species has been utilized directly as a fishery resource, though they have been shown to be an important food of several exploited cetaceans including southern right, humpback, sei and blue whales. In addition, they are important in the diet of many rock-fish, seals and several species of sea-birds. It is to be expected that systematic trawling in sub-Antarctic waters will indicate large benthic stocks of both these species. By analogy with other species discussed below, they are unlikely to confine themselves to rocky substrates where trawling is impossible.

3 HUMBOLDT CURRENT RESOURCES

3.1 Biology

To the north of the region occupied by the two species of Munida described above, there occur two species which do not appear to have a postlarval pelagic phase. These are the 'langostino amarillo', Cervimunida johni, and the 'langostino colorado' or 'zanahoria', Pleuroncodes monodon, both of which have mass occurrences in the benthos off the Chilean coast. Méneville noted the occurrence of pelagic galatheids in the harbour of Callao in 1830, during the cruise of LA COQUILLE round the world (in H. Milne Edwards, 1837), but there appears to be no other evidence of a pelagic phase in these species. The Callao specimens appeared to belong to the then-valid genus Grimothea though Méneville's illustrations are not very satisfactory. U.S. tuna fishermen, very familiar with the pelagic phase of P. planipes, know of no similar form from the Peru Current, though the benthic phase of P. monodon appears to extend as far north as Central America.

The benthic concentrations off Chile, where they are best known, appear to be comprised of individuals of both species within the same size range. Specimens have a mean weight of about 25 g and carapace lengths ranging from about 20 to 40 mm. This is about the same size as the benthic adults of M. gregaria discussed above (2.1). Shrimps of commercial importance may occur on the same grounds, but usually the mass occurrences of galatheids do not appear to correspond with the most dense populations of penaeids (Mistakidis and Henriquez, 1966).

3.2 Range of benthic phase

The Chilean shrimp fishery, which includes a fishery for these two galatheids, has defined their range as extending approximately from Caldera in the north to Calbuco in the south, though the whole of this zone has not yet been properly explored (Lopez-Capont et al., 1965). Within this zone, the largest concentrations of langostino appear to occur within the depth-range 125 to 200 m. In the same depth-range the abundant shrimp appears to be Heterocarpus reedi, although below about 150 m the galatheids overlap the range of the deep shrimp ('gamba') Hymenopenaeus diomedeae. Gallardo (1963), in his study of the benthic communities off the Chilean coast, recognizes a lower sublittoral zone, extending from 50 to 400 m in which the biomass is very low and in which the bottom water is very deficient in oxygen. This is the result of the well-known oxygen minimum layer (e.g. Brandhorst, 1959) of the eastern Pacific Ocean meeting the continental slope, and similar conditions appear to extend along much of Central America. They will be referred to again below in connection with the distribution of the Mexican species of Galatheidae. It appears that P. monodon and C. johni must be capable of supporting mass populations in water with dissolved oxygen values as low as 0.1 ml/l. It is noteworthy that Gallardo describes the deposits in these zones as being of soft, highly organic substrata probably derived from the sinking of diatom cells from surface blooms. These blooms are associated with the upwelling areas so typical of this coastline.

3.3. Exploitation

The fishery for these galatheids has been prosecuted since 1953, and has reached an annual catch of 10×10^3 tons annually (Table I).

TABLE I

The development of the Chilean 'langostino'
landings (from Lopez-Capont, et al., 1965)
Units = metric tons

	Total catch	Consumed fresh	Canned	Frozen tails
1953	0.93	0.29	0.59	0.47
1954	2.64	0.85	1.20	0.58
1955	2.05	0.78	1.10	-
1956	5.71	1.61	3.57	-
1957	11.38	4.27	0.73	5.82
1958	12.83	5.37	0.22	6.33
1959	6.75	0.93	0.80	5.02
1960	8.12	1.22	0.83	6.02
1961	8.15	0.62	0.65	6.89
1962	7.99	0.36	0.94	6.69
1963	9.25	0.20	0.94	7.91
1964	10.67	0.68	0.94	9.03

In the early years of the fishery the landings were generally utilized in the fresh state or as a canned product, but at the present day almost the entire landings are frozen for export. The landings comprise about 60 percent C. johni (Mistakidis and Henriquez, 1966), but this may not be an accurate reflection of relative abundance in the sea. C. johni has a slightly higher meat yield (9 to 10 percent) than has P. monodon (6 to 7 percent), and there may well be a preference for it in the fishery.

There is a seasonal fluctuation in the landings, which are normally highest during the first half of the year (Lopez-Capont, et al., 1965). The small trawlers used in the fishery average about 0.6 ton/h, but recent surveys have shown that catch-rates may, on occasion, go much higher than this average. Maximum catch-rates, obtained during a survey to the north of Constitución (Mistakidis and Henriquez, 1966), were 4.16 ton/h at 36 to 37°N and 2.53 ton/h at 35 to 36°N.

It seems likely that this resource extends a good deal further to the north than it is currently exploited, for P. monodon is known to extend along the Peruvian coast as far north as the Lobos de Afurea Islands (Haig, 1955). There is even evidence of its occurrence off the west coast of Mexico, at Acapulco (Boyd, MS), though this record, together with Boyd's discussion of specific characters, suggests that the distinction between P. monodon and P. planipes requires further examination.

4 CALIFORNIA CURRENT RESOURCES

4.1 Biology

The red or pelagic crab, Pleuroncodes planipes, occurs at the southern end of the California Current and in the Gulf of California in both the benthic and pelagic phases. Mass occurrences of the pelagic phase in the surface waters are a well-known phenomenon in this region, and although it occurs at least 1,000 mi to the southwest of Baja California in the extension of the California Current, it does not appear to extend southwards along the coast of Mexico far below the mouth of the Gulf of California.

Until relatively recently the benthic phase was unknown, but it is now established that it occurs widely on the upper parts of the continental slope, both in the Gulf and along the western coast of Baja California (Boyd, MS; Parker, 1964; Perkins, personal communication). Boyd found benthic P. planipes along this coast to 26°N, while Parker found them to 28°N in Sebastian Viscaino Bay, and this appears to be their northern limit in normal years. Parker, however, found them as far as latitude 32 to 33°N, in the area of Ensenada and San Diego, during the warm year 1959 to 1960, a range extension which will be discussed below.

The data on the depths at which P. planipes have been found in the benthic phase by these three authors are consistent, as the following tabulation indicates:

	Depth (m)	T°C	O_2 (ml/l)
Boyd	75-300	10.0-14.0	0.5
Parker	64-366	9.0-14.0	0.5-2.0
Perkins	73-201	12.0-14.6	

Further ecological data on the associated fauna of stations at which P. planipes occurred, given both by Boyd and Parker, indicate that mass concentrations occur to the virtual exclusion of other forms. Parker writes of enormous numbers of Pleuroncodes (together with an unidentified species of Munida) occasionally occurring in a depth zone otherwise largely devoid of benthic organisms, and in which occurred large quantities of undecayed organic detritus at the surface of the deposits. As with the Chilean species, all benthic records of P. planipes are from depths corresponding to the oxygen minimum layer, and this is confirmed by the actual observations of oxygen concentration tabulated above. It is suggested that the mass occurrences often, or usually, occur on the deposits underneath coastal upwelling regions and other places in which diatom blooms occur. The 'rain' of Coscinodiscus and other diatom cells in these areas produces green, unoxidized muds, with a very high organic content, which are probably utilized as food by the benthic galatheids. Aquarium observations of P. planipes show that, as well as feeding as a predator on almost any organism of suitable size, it will readily feed on organic detritus lying on the bottom of the vessel. It sweeps detritus towards the mouth by the action of the fan-shaped third maxilliped.

There do not appear to be any significant morphological differences, apart from size, between pelagic and benthic individuals of this species. The pelagic phase is as regular an occurrence in the life history of P. planipes as is the grimothea stage of M. gregaria. The third maxilliped is foliaceous and the walking legs have a fringe of natatory setae in both the benthic and the pelagic phases. It seems probable that in P. planipes there can be an alternation between pelagic and benthic phases in the life of a single individual.

4.2 Range of pelagic phase

The distribution of the pelagic phase of P. planipes in the California Current is now well known, both as a result of special investigations and of the long-term plankton studies of the California Cooperative Oceanic Fisheries Investigations. Fig. 1 and 2 are derived from the latter data and indicate the frequency of occurrence of pelagic swarms in different regions off the California coast and the oceanic areas in

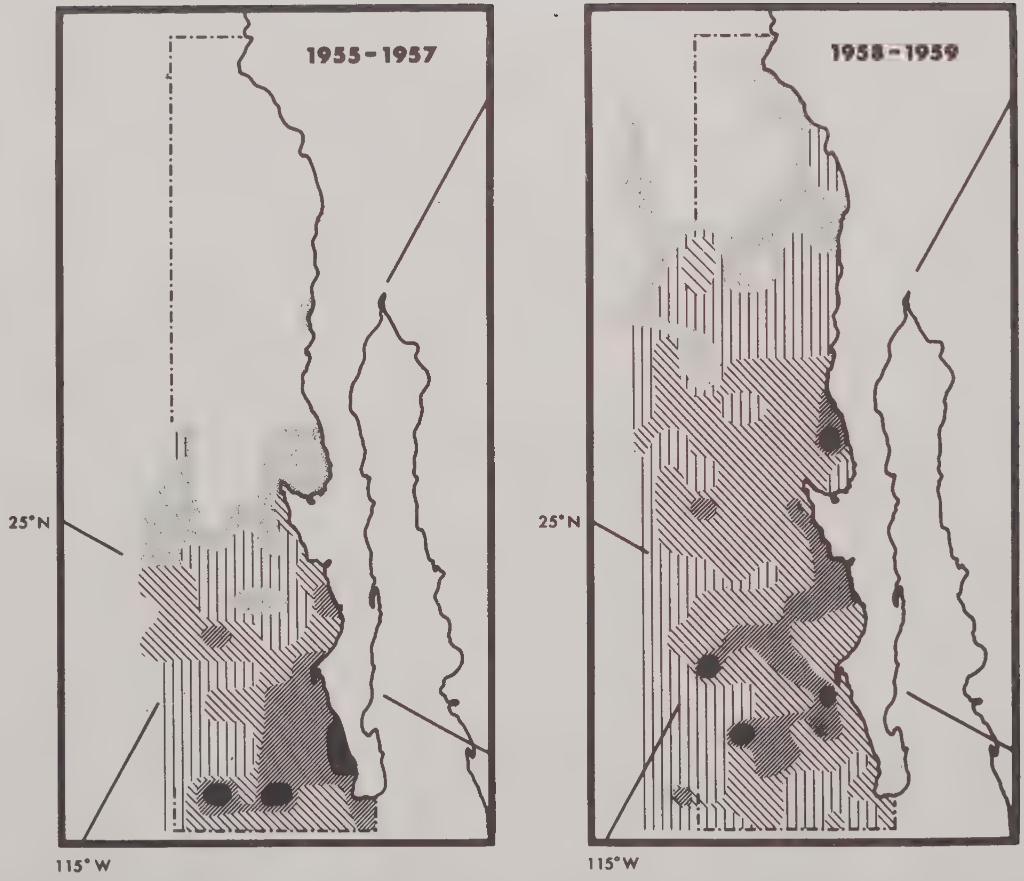

1955-1957
1958-1959
25°N
25°N
115°W
115°W

Fig. 1 Distribution of Pleuroncodes planipes in pelagic phase in California Current, expressed as percentage occurrence in plankton hauls at standard CalCOFI stations. Shaded areas (lighter to darker) represent: 1-10%, 11-25%, 26-50%, 51-75%, 76-100% occurrence.

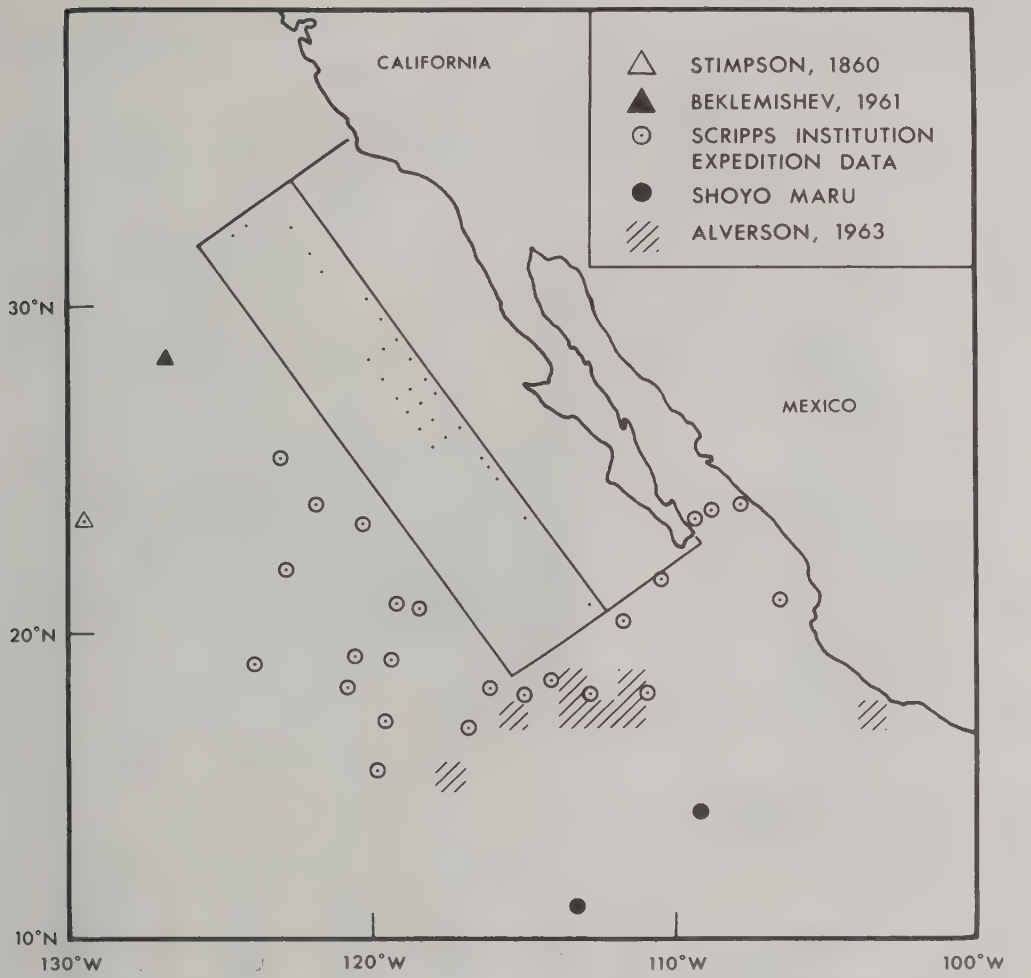

CALIFORNIA
STIMPSON, 1860
BEKLEMISHEV, 1961
SCRIPPS INSTITUTION EXPEDITION DATA
SHOYO MARU
ALVERSON, 1963
MEXICO
30°N
20°N
10°N
130°W
120°W
110°W
100°W

Fig. 2 Distribution of Pleuroncodes planipes in pelagic phase in offshore and oceanic regions of California Current. Coastal rectangle is area illustrated in Fig. 1; outer rectangle was sampled regularly but less frequently (occurrences indicated by dots); other records from irregular or occasional observations.

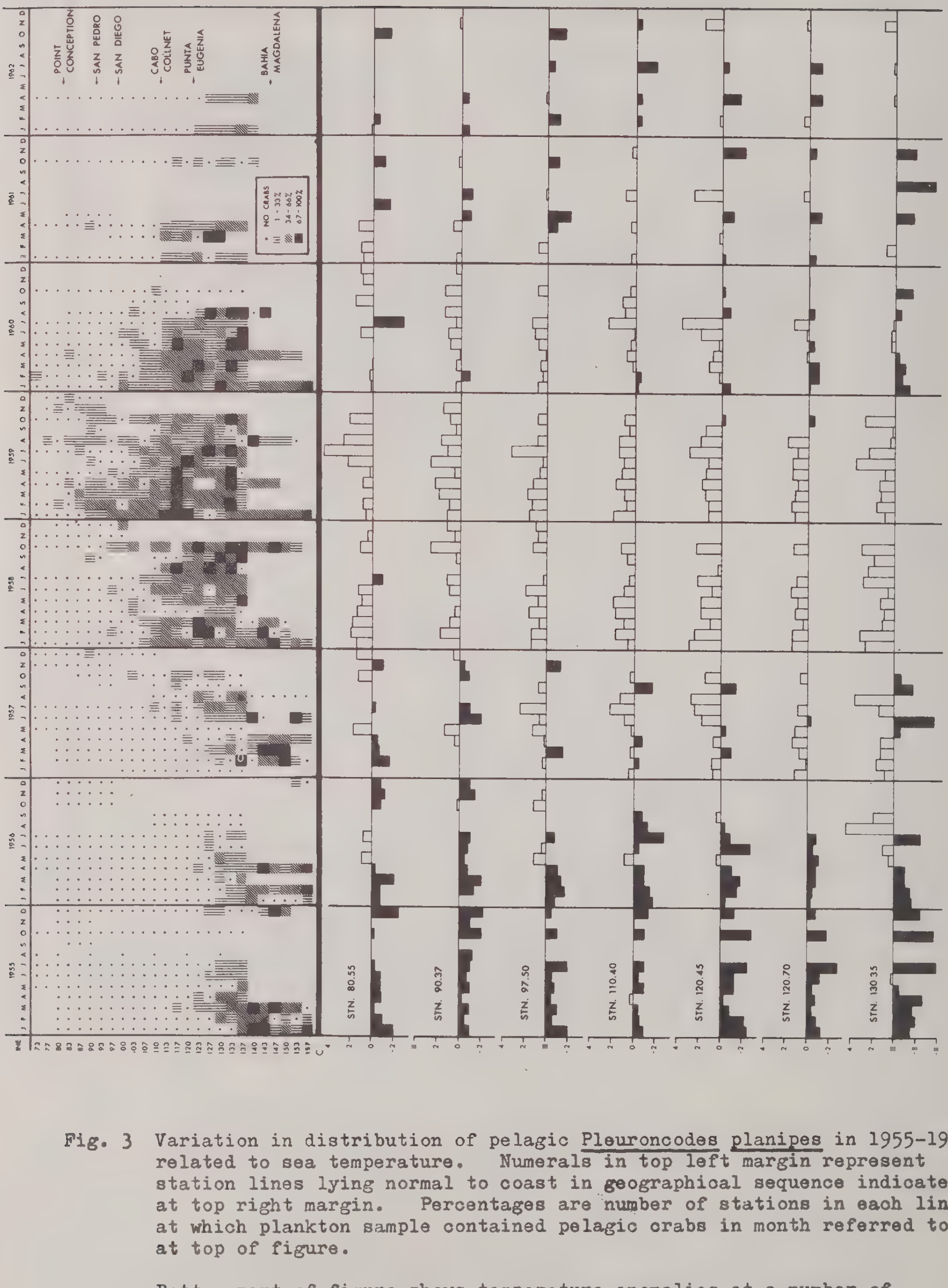


Fig. 3 Variation in distribution of pelagic Pleuroncodes planipes in 1955-1962 related to sea temperature. Numerals in top left margin represent station lines lying normal to coast in geographical sequence indicated at top right margin. Percentages are number of stations in each line at which plankton sample contained pelagic crabs in month referred to at top of figure.

Bottom part of figure shows temperature anomalies at a number of selected stations.

which smaller numbers of specimens have been recorded. The swarms appear in regions of coastal upwelling, and there is some dispersal in the waters of the offshore drift, to the southwest of the California Current.

Also indicated (Fig. 3) is the manner in which the range of the pelagic phase off the western coast of Baja California changed in response to the changing climate in the years 1955 to 1962. Pelagic crabs were recorded abundantly as far north along the Californian coast as the Monterey Peninsula in 1960. Both the range extension to the north at the start of the warming period and the regression at the end of the period can be explained (Longhurst, in press) by the changing patterns of flow in the California Current at these times, particularly the changing form of the large permanent gyre which normally exists to the south of Point Conception. During this northerly range extension, there were numerous records of windrows of pelagic P. planipes being swept ashore at points along the coast of California, a phenomenon which is of common occurrence along Baja California and the Gulf coasts, and which recalls the reports of strandings of M. gregaria described above (Glynn, 1961; Boyd, MS; Radovich, 1961; Longhurst, in press).

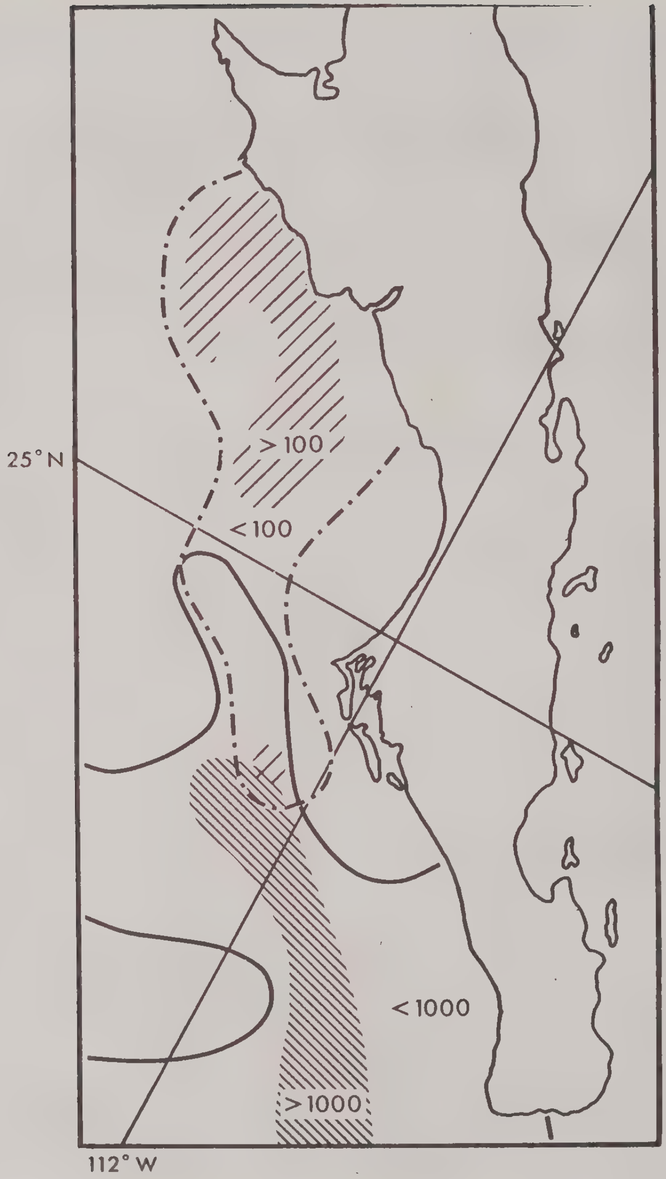
The problem of the relationship between the pelagic swarms and the benthic populations along the continental slope is an interesting one and hard to resolve. It is evident from the general pattern of flow at the southern end of the California Current that there is an offshore drift to the southwest in the surface waters. The distribution of the pelagic phase in oceanic areas suggests that pelagic specimens from the coastal areas of Baja California are swept offshore by this drift. The flow of the California Current is far from laminar (Reid, Schwartzlose and Brown, 1963) and sufficient eddying occurs to maintain a spat-fall of planktonic larvae of benthic organisms along the continental shelf. There is evidence, however, that the larval forms of P. planipes are flushed out of the Baja California centers of spawning (Fig. 4) into oceanic areas to the southwest. It has also been demonstrated (Longhurst, in press) that the pelagic postlarval forms in oceanic areas are generally smaller than those encountered in massive swarms over the continental shelf, and both these groups are generally larger than the individuals encountered in the benthic phase (Boyd, MS; Longburst, in press).

The question to be resolved, therefore, is whether or not the oceanic individuals in the pelagic phase are lost to the parent stock on the continental slope, or whether they (or a proportion of them) return to coastal areas. The evidence is conflicting: a possible mechanism for their return exists in the sub-surface currents flowing to the northeast under the California Current, and closing-net tows have shown concentrations of crabs at the right depths for such transport (Longhurst, in press), but there is recent evidence that maturity is reached by some pelagic individuals in the oceanic region and that breeding occurs there (Blackburn, personal communication). Perhaps both possibilities are partly true. It is particularly difficult to determine whether or not an alternation occurs between benthic and pelagic phases over the continental shelf, but the fact that benthic individuals retain their natatory setae is evidence for such an alternation. Individuals captured at sea in the pelagic phase are very ready to adopt a benthic existence again, and can be seen clinging to any substrate which they encounter; it is not unusual to bring one up clinging to an oceanographic instrument, they have been observed clinging to large salps in the upper few metres of water, and they settle at once in an aquarium.

4.3 Food relationships

The ability of P. planipes to graze directly upon blooms of phytoplankton with a major diameter in excess of 25 to 30 μ has recently been demonstrated and the filtering mechanism described (Longhurst, Lorenzen and Thomas, in press). The aperture size of the filter formed by the exopodites of the third maxillipeds appears to correspond with the minimum particle size retained during experimental grazing on natural phytoplankton, and is of the order of 25 μ in Pleuroncodes of approximately 20 mm carapace length.

Pelagic individuals can be watched at sea from an underwater observation chamber, and it can be seen that they graze by using their fan-shaped maxillipeds as a cast-net


>100
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25° N
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112° W

Fig. 4 Distribution of larval (dotted line) and megalopa (solid line) forms of Pleuroncodes planipes off Baja California in June 1964.

while they are sinking slowly with their legs spread out like a parachute. A grazing population comprises many individuals slowly sinking in this way, interspersed with others swimming rapidly upwards by abdominal flexure. Animals that have become accustomed to an aquarium can be induced to graze even when they are resting on the bottom.

Experimental data show that a large volume of water can be filtered during grazing. The maximum daily production of faecal pellets recorded for a freshly-caught grazing crab amountedto 102 mg dry weight and consisted of greenish material in which 5×10^5 whole undigested cells of Coscinodiscus were counted. Under the natural standing crop conditions observed, this would correspond to 540 l/day filtered, assuming a filtration efficiency of 100 percent and a digestive coefficient of 50 percent. Calculations based on close observation of the rate of beat of the filtering appendages produce an estimate of the maximum filtration rate of 432 l/day. The two figures are in general agreement.

The above observations were made off Baja California, and the grazing budget of the same location was monitored over a five-day period. The results suggest that herbivorous zooplankton was responsible for only about 10 to 15 percent of the observed excess of phytoplankton production over the observed standing crop, and that the stock of pelagic crabs was sufficient to be responsible for most of the remaining apparent grazing. Evidently the pelagic phase of P. planipes may play a very important role in the grazing of diatom blooms in coastal upwelling areas in the California Current.

The importance of Pleuroncodes in the diet of many predatory animals in this area is well known. The fish Eschrichtius, Neothunnus, Thunnus, Katsuwonus, Coryphaena, Seriola, and the birds Larus, Phalacrocorax and Pelecanus all feed actively on mass occurrences of pelagic crabs (Longhurst, Lorenzen and Thomas, in press). Alverson (1963) has demonstrated that the stomach contents of yellowfin tuna (Neothunnus albacares) from the region to the west of Baja California were dominated by pelagic Pleuroncodes; the mean volume of crabs contained in each yellowfin stomach was about 0.5 l (or about 100 crabs). This figure must be less than the average daily intake of each member of the population of tuna, and 3.99×10^6 tuna were taken by the United States fishery alone in 1960 off Baja California. This represents a daily cropping at the beginning of the season of 2×10^3 tons of Pleuroncodes by those fish which would be caught by the fishery in the subsequent six months or so. The quantity utilized by this single stock of predatory fish is thus very high indeed over the year as a whole.

The main ecological significance of the utilization of pelagic Pleuroncodes in this manner is that the food-chain is thus rendered unusually short and direct between the primary producers and the climax predators.

In the offshore oceanic environment, the pelagic crabs maintain themselves on a more varied diet than over the continental shelf. Food is obtained both by the filtration apparatus and also by selective particulate feeding by use of the chelipeds; it consists mainly of small Copepoda (Microsetella, Clausocalanus, etc) and large Protozoa (radiolarians, tintinnids), together with a few large phytoplankters such as dinoflagellates. A survey of stomach contents from a grid of stations to the west of Baja California in June 1964 showed that it was only in a relatively few localities that phytoplankton dominated the stomach contents and that these stations were situated in upwelling areas.

4.4 Breeding and growth

Breeding occurs in the California Current during the winter months, especially in the first three months of the year; this is evident from data of Boyd and Johnson (1963) on the percentage of ovigerous females in the CalCOFI plankton samples, and is confirmed by work now in progress on the distribution of larval forms in the same plankton samples. The five larval stages described by Boyd (1960) are passed through in 3 or 4 months in the laboratory (Boyd and Johnson, 1963), and this is essentially confirmed by studies on net-caught larvae.

The work in progress indicates that breeding is concentrated at a few centers over the continental shelf, and it is presumed that these correspond with the centers of distribution of the adult crabs as a whole, including both benthic and pelagic stocks.

Growth rates of the postlarval forms have been studied both by Petersen's method on net-caught samples and in the laboratory (Boyd, MS). In general terms, a carapace length of about 20 mm is attained at the end of the first year, a little less than 30 mm at the end of the second year, and about 35 mm at the end of the third year. There are reasons to suppose that growth rates are not constant over all the ecological situations in which the species occurs. The approximate growth rates just given, however, suggest that the benthic stocks are in their second and third years of life (the deeper, the older), the pelagic stocks over the continental shelf are between 9 and 15 mo old, and the offshore oceanic stocks are within their first year of life. There may be an underestimation of the age of offshore stocks as these will be living at a lower nutritional level than the inshore stocks.

4.5 Exploitation

There has been no exploitation of this species directly, but the possibility of such exploitation is clear, and food-processing interests in California are currently studying the viability of a fishery for P. planipes.

One of the first decisions to be made in planning such a fishery is whether the exploitation should be based upon the pelagic or the benthic phase of the species, or upon both. Unfortunately, the data for an entirely rational decision do not at present exist, for no comprehensive trawling survey of the region has been completed to determine the real extent of the benthic stocks, nor their seasonal variation. One of the major problems to be solved currently is the fate of the pelagic stocks over the continental shelf which are generally considerably more abundant early in the year. Have they been flushed out to sea, have they been grazed down by the migratory tuna which arrive in the area in the spring, or have they descended and been recruited to the benthic stocks?

Blackburn (personal communication) has observed the density of pelagic swarms to be very variable, from situations where the crabs are exceedingly sparse to those in which they appear to be piled up on top of one another. During several cruises to the region of Baja California in which standard tows were made with a nekton net on a standard grid system, a total of 33 hauls collected pelagic Pleuroncodes, at a mean density of 101.7 ml of crabs per $10^3 m^3$ of water filtered. At 32 of these stations the volume of crabs was from 1 to 355 ml/$10^3 m^3$, while at one station it was 1539 ml/$10^3 m^3$; such a distribution confirms subjective observations at sea, which suggest that the most dense mass occurrences are denser by almost an order of magnitude than the 'background' occurrences of pelagic individuals. It can be supposed, therefore, that by searching it would be possible to find concentrations that would yield 250 kg/h with a small pelagic trawl; this figure is based on a mouth aperture of $30 m^2$, a towing speed of 5.4 km/h, and a filtration efficiency of 100 percent. This figure is likely to be an underestimate, since the density of individuals on which it is based was taken from a net worked on a standard oblique haul to 200 m depth and which was not held at the depth at which crabs were seen or thought to be aggregated. My observations at sea suggest that, at times, it would be possible to exceed this figure by a factor of ten, by selective fishing with such a net.

The data of Boyd (MS), Parker (1964) and Perkins (personal communication) on the benthic phase include some estimations of the population density of individuals. Using a swept area method based on the catch of a trawl having an aperture approximately 3 m wide, Boyd suggested that the average density at one station was of the order of 10 Pleuroncodes per m^2 on the deposits. Extrapolating to a commercial otter trawl of 10 m across the mouth and a towing speed of 5.4 km/h, this implies a catch rate of 13.5 x 10^3 kg/h, assuming a catching efficiency similar to that of Boyd's 3 m trawl. At such a high catch rate it would be impossible to tow a demersal trawl for as long as one hour without it so filling with crabs as to be torn or lost altogether. This has, in fact, been the experience of a trawling survey along the west coast of Baja California. Perkins (personal communication) found that during a trawling survey for demersal fish along the continental shelf it was impracticable to trawl deeper than about 150 m along much of the coastline since the trawl rapidly filled with benthic Pleuroncodes and became unmanageable. This first estimate of likely catch rates in a demersal fishery for Pleuroncodes cannot be more than preliminary, and may be considerably modified by a properly conducted survey of the benthic crab resources, and such a survey is urgently required before any rational planning of a fishery can take place. In any case, the available evidence suggests that catch rates at least as high as those which prove to be economically feasible in the Chilean fishery may be obtained off Baja California.

5 POTENTIAL OF THE RESOURCES

As part of the FAO participation in the Indicative World Plan for Agricultural Development, estimates of the total potential yield from fisheries resources are required, and it is interesting to postulate what might be the long-term annual yield from the utilization of mass occurrences of galatheids. The estimate is restricted to the three regions discussed here, and ignores any further stocks which may in the future be identified in other eutrophic ocean areas. It leans rather heavily on the figure of 10×10^3 tons for the present annual landings of the Chilean fishery and assumes approximately equivalent biology and size of individuals in the various species concerned. It is suggested that the potential yield is most unlikely to be less than 30×10^3 tons per annum. It may be higher than this figure: a factor of ten times seems subjectively just possible, while a factor of one hundred seems impossible. It is suggested therefore that the ultimate yield from the stocks considered here will be found to lie between 30×10^3 and 300×10^3 tons per annum. To attempt a narrower estimate than this would be quite unrealistic, in our present state of ignorance about the real extent of the benthic stocks of two of the five species under consideration.

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FERTILIZATION AND COMPLETION OF MEIOSIS IN SPAWNED EGGS OF THE AMERICAN OYSTER, *CRASSOSTREA VIRGINICA* GMELIN

A. CROSBY LONGWELL and S. S. STILES
Bureau of Commercial Fisheries Biological Laboratory, Milford, Connecticut 06460

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It is of fundamental importance to an understanding of the genetic system of the commercially valuable American oyster, *Crassostrea virginica* Gmelin, to know whether its meiosis is of the normal type found in the vast majority of metazoa or one of the various anomalous types. These anomalous forms have developed in particular groups in association with parthenogenesis or male haploidy, and even in some groups with a bisexual method of reproduction and diploidy in both sexes (WHITE, 1954). Protandry and hermaphroditism are common in the Mollusca (WHITE, 1954).

Irrespective, however, of whether they are normal or atypical, cytogenetic knowledge of meiosis and fertilization in the American oyster is indispensable to its genetic study and selective breeding. Such information is particularly important because eggs like those of this bivalve mollusk, which are fertilized externally and complete maturation after fertilization, are especially susceptible to wide variations of one or both maturation divisions (WILSON, 1953). Laboratory and hatchery rearing of oyster larvae depends on laboratory-stimulated development of the gonads of adult animals, proper maturation or meiosis of the eggs, and successful fertilization of normal eggs from induced spawnings (LOOSANOFF and DAVIS, 1963).

Early cytological studies of the chromosomes, cell division, and development of marine eggs (see WILSON, 1953, for review) did not include any critical studies of the Ostreidae. In more recent years marine animals have not been much considered in cytogenetic researches even though improvements in chromosome techniques (SHARMA and SHARMA, 1965) have removed many of the methodological obstacles to their cytological study.

An illustrated account is presented here of the completion of meiosis and fertilization in mature, spawned eggs of *C. virginica*; it is based on the study of thousands of eggs from numerous crosses of gametes of different

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parents. Observations were supplemented and confirmed over a period of a year while we were preparing a karyotype of the American oyster chromosomes and in the course of other genetic studies (LONGWELL *et al.*, 1967).

MATERIALS AND METHODS OF PREPARATION

All oysters were from wild *C. virginica* stock local to the vicinity of the harbor of New Haven, Connecticut. Eggs and the sperm used to fertilize them came from thermal-induced spawnings of adult male and female oysters conditioned in the laboratory for spawning (LOOSANOFF and DAVIS, 1963).

Oysters of the oviparous *Crassostrea* species are usually not hermaphroditic and functional eggs and sperm are only rarely found together. Age and environment, however, affect the frequency of hermaphroditism in these oysters. *C. virginica* is protandric and the degree of protandry varies greatly among juvenile, 1-year-old oysters in their first breeding season (GALTSOFF, 1964).

Fixation was in Carnoy's fluid (ethyl alcohol: glacial acetic acid, 3:1) for a few minutes to several days. Squashes were made in 1-2% orcein in 45-60% acetic or proprionic acid.

Before squashes were made, yolk was extracted from the eggs in a micro Soxhlet apparatus with a 1:1 mixture of methyl alcohol and chloroform. The usual extraction time approximated 2 hours (LONGWELL and STILES, 1968).

Eggs were examined and photographed with a 100X Zeiss Neofluar phase-contrast objective.

REGULAR MEIOSIS AND FERTILIZATION IN SPAWNED EGGS OF THE AMERICAN OYSTER

Normal, unfertilized, spawned eggs of *C. virginica* are either at Prometaphase or Metaphase I of meiosis. Occasionally a spawned egg is at Diakinesis (Fig. 1) or late Diplotene. Few unfertilized eggs proceed beyond Metaphase I.

Fig. 1. — Ten pairs of Diakinesis chromosomes of an unfertilized egg of *C. virginica*. ×2100.

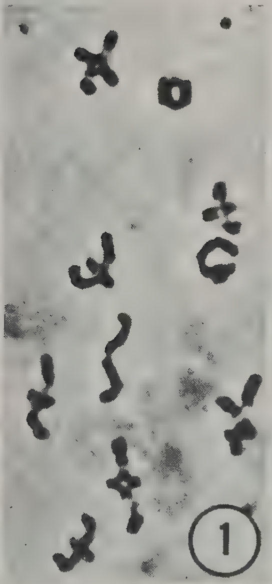
Fig. 2. — Metaphase I bivalents of a *C. virginica* egg with the round, dense sperm nucleus at the right of the metaphase plate (at arrow). ×2000.

Fig. 3. — Late meiotic Anaphase I in a *C. virginica* egg showing the reduced number of chromosomes and the male pronucleus (at arrow). ×2250.

Fig. 4. — Portion of an egg of *C. virginica* showing a Metaphase II chromosome group, first polar body nucleus (to the right of the metaphase group), and chromosomes developing from the male pronucleus (group at lower left). ×2500.

Fig. 5. — The 10 highly contracted Metaphase II chromosomes of a *C. virginica* egg. (Two chromosomes are lying close together). ×2500.

Fig. 6. — The two polar body nuclei of a fertilized egg of *C. virginica*. One has a more diffuse and irregular outline than the other. ×2100.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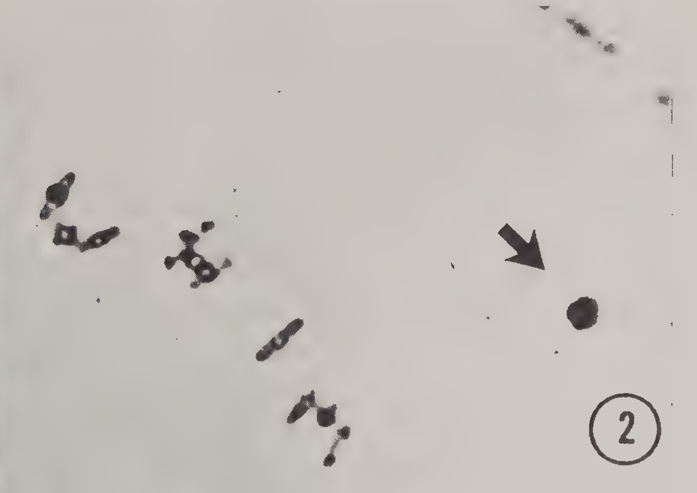
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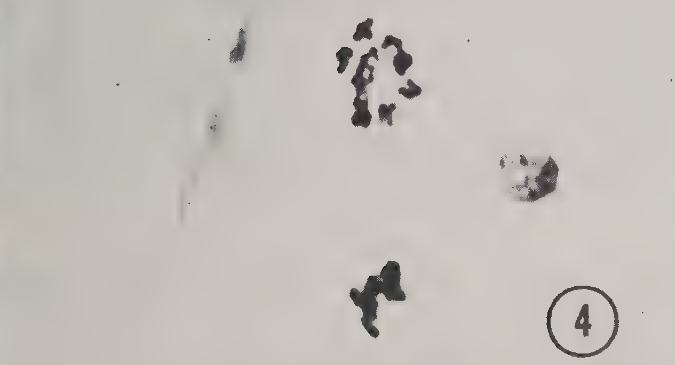
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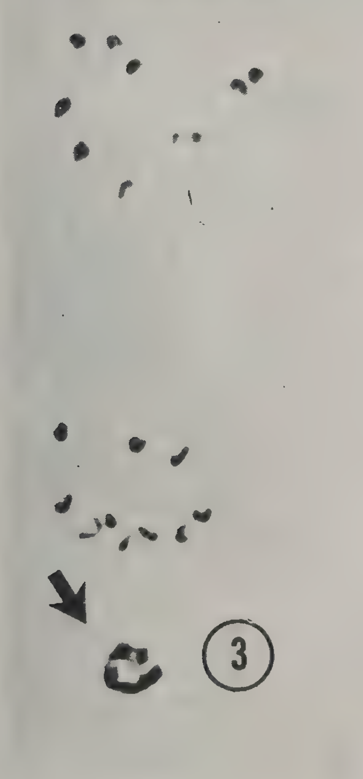
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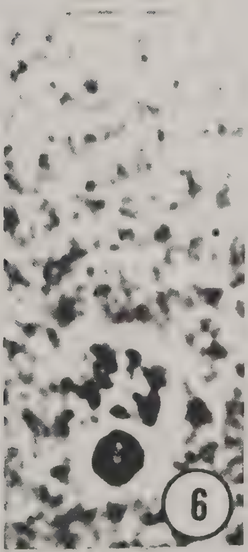
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Immediately after fertilization the dense, compact sperm head is clearly recognizable in the egg cytoplasm. The size of this sperm head soon begins to increase. Figure 2 shows the 10 bivalents of the female aligned across the Metaphase I spindle and the swollen but still dense sperm nucleus lying to one side of the division group.

Once fertilized the eggs rapidly proceed to complete meiosis.

The first meiotic division is reductional. Each Anaphase I group has 10 chromosomes (Fig. 3).

About Telophase I of the female gamete the sperm nucleus has been transformed into the diffuse, vesicular male pronucleus, which soon takes the general appearance of a prophase (Fig. 3).

One of the Telophase I groups forms the first polar body nucleus (Fig. 4). The other Telophase I chromosomes pass directly into the equational plate of the second meiotic division with its 10 super-contracted chromosomes (Figs. 4 and 5).

The second, innermost polar body nucleus is formed from one of the Telophase II groups. Figure 6 illustrates the two polar body nuclei. These nuclei are extruded from the eggs and constricted off them with a small portion of cytoplasm.

During Division II of the female gamete, the male pronucleus gives rise to the 10 chromosomes of the male parent.

No prolonged female pronuclear stage was observed.

The chromosomes of the egg and sperm are combined in one group through their orientation on the first cleavage spindle. For some time before this stage and to the onset of the first cleavage, the prometaphase chromosome sets of the male and female gametes are readily distinguishable from one another by virtue of the differences in their position in the egg. Individual chromosomes of each group can be conveniently and easily studied at this stage. At this time the chromosomes of the female tend to be more elongated than the usually shorter, denser chromosomes of the male gamete (Fig. 7). Once they are fully oriented on the metaphase plate the chromosome set of each gamete is equally contracted. This stage is reached approximately 1 hour after the addition of the sperm suspension to the eggs.

As cleavage begins, the presence of two polar body nuclei and the

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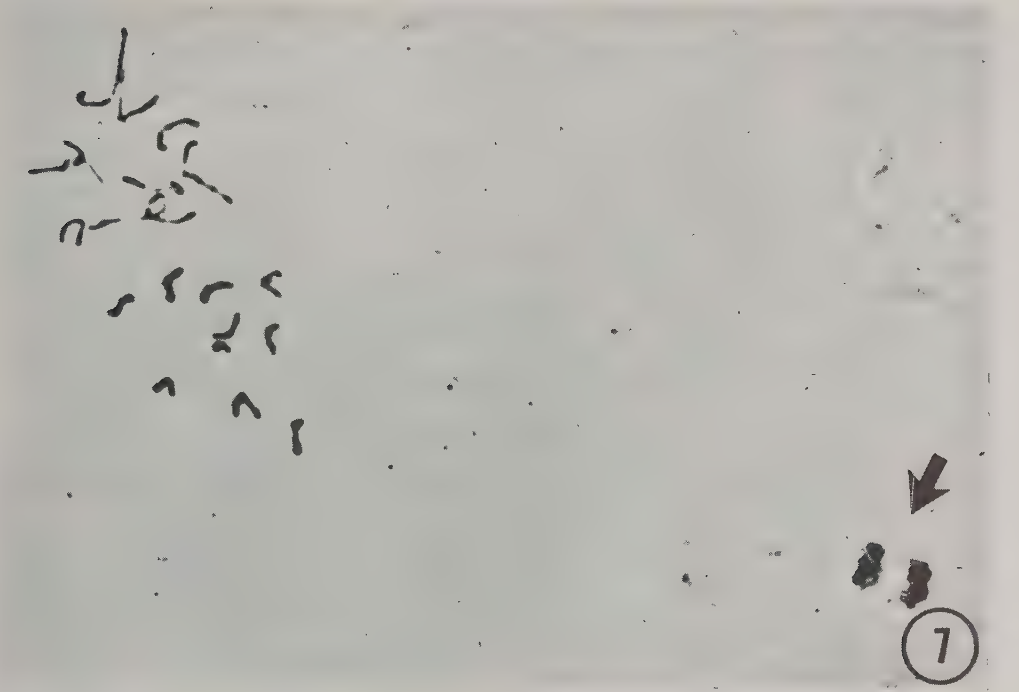
Fig. 7. — The haploid chromosome sets of the male and female gamete of *C. virginica* just before their coming together on the first cleavage spindle. The 10 more elongated chromosomes of one group are the female chromosomes; the 10, shorter, denser chromosomes are the group brought into the egg by the sperm. To one side of the photomicrograph are the two polar body nuclei (at arrow), an indication of normal meiosis. ×1600.

Fig. 8. — First cleavage anaphase in a *C. virginica* egg after successful completion of meiosis and fertilization (normal chromosome number and normal polar body nuclei — to the left of the egg). ×1600.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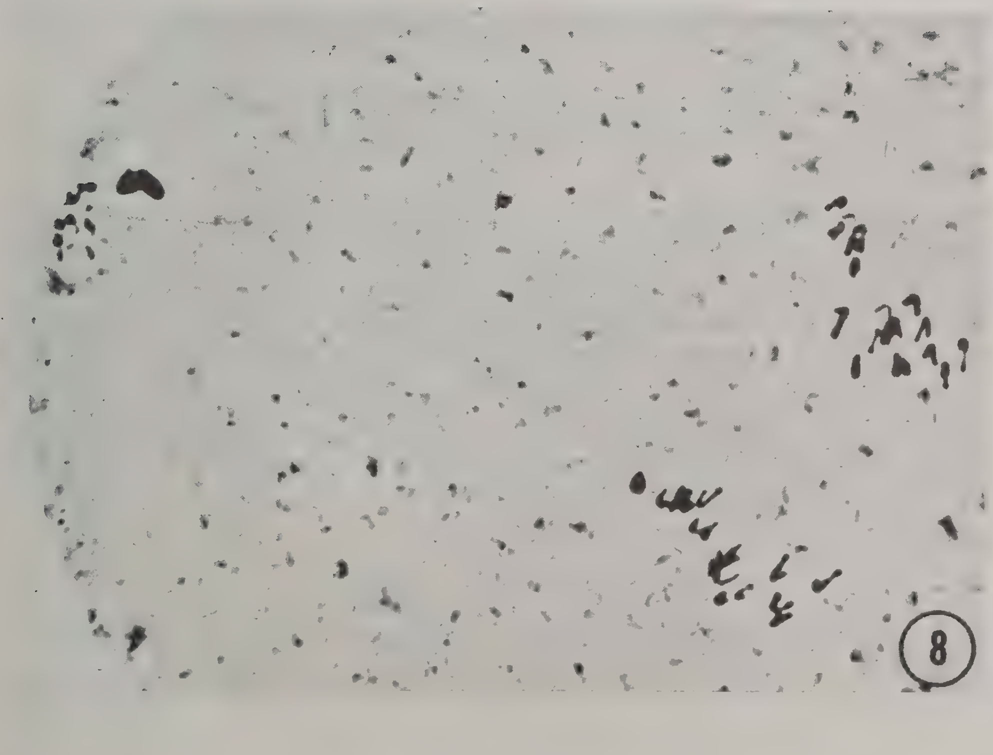
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absence of any other nuclear group in the egg aside from the cleavage chromosomes indicate that meiosis and fertilization were at least superficially normal (Fig. 8). Figure 9 shows a somewhat later cleavage embryo with its two polar body nuclei.

The first, outermost polar body enters division usually at the 64-cell stage of the embryo. In abnormal eggs this nucleus tends to begin dividing earlier. This division has the appearance of a colchicine metaphase with much contracted easily studied chromosomes (10) and no organized spindle (Fig. 10). These polar body chromosomes have never been observed to enter anaphase, although embryos were studied cytologically until just before the emergence of the trochophore larvae at which time the polar bodies are lost.

Sometimes it seems to be the second, innermost polar body nucleus that enters this abortive mitosis. No eggs have ever been observed in which both polar body nuclei are in division.

Karyotype studies on early cleavage chromosomes of this oyster (LONGWELL *et al.*, 1967) have shown them to be about 2 to 3.5 microns long at colchicine metaphase. No unusual phenomena are associated with early cleavage.

Thus far, meiosis in male oysters has been only cursorily examined. It also seems to be of the normal type. The small size of the spermatocytes, however, impedes their analysis.

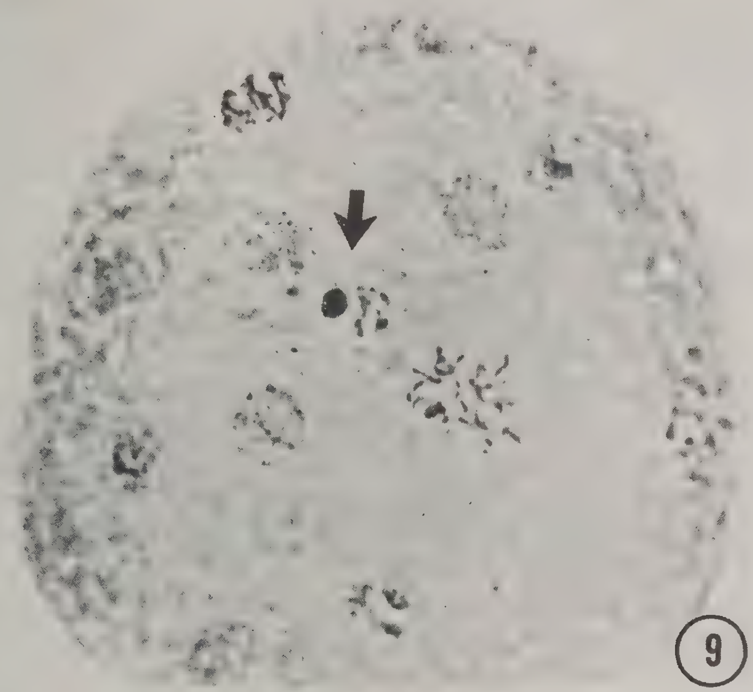
IRREGULAR MEIOSIS AND FERTILIZATION IN SPAWNED EGGS OF THE AMERICAN OYSTER

Various deviations from the usual sequence of these events of meiosis and fertilization were not infrequent in the material used in this study. Aneuploid, haploid, triploid, tetraploid, and chromosomally mosaic embryos are the result of such disturbances. They no doubt lead to poor embryo and abnormal larval development, and death in a significant number of cases.

Polyspermy can occur in *C. virginica* and more than one sperm nucleus can be resolved into chromosomes in a single egg. These extra nuclear groups can either remain *in situ* in the cytoplasm or several of them may fuse with the female group with the resultant formation of a multipolar spindle.

Fig. 9. — Early cleavage embryo of *C. virginica* showing its two polar body nuclei (at arrow). ×1200.

Fig. 10. — Metaphase of a polar body (at arrow) division in a *C. virginica* egg. Seven of the 10 chromosomes show at the level of focus at which this photomicrograph was taken. ×1600.



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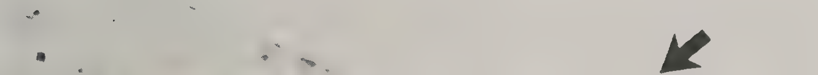

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The incidence of parthenogenesis is low and variable in eggs of our local, wild oysters conditioned and spawned under laboratory conditions. A Metaphase I group in unfertilized eggs of the American oyster occasionally begins, after some time, to divide equationally. The two products of the female second meiotic division sometimes fuse in fertilized and unfertilized eggs alike. Some unfertilized eggs complete meiosis normally and then with only the female set of chromosomes commence to cleave.

COMPARISON OF MEIOSIS AND FERTILIZATION PHENOMENA AMONG MOLLUSCAN AND OTHER EGGS

As in the eggs of *C. virginica*, maturation of most other molluscan eggs begins spontaneously after spawning in sea water with the breakdown of the germinal vesicle (RAVEN, 1958). Like this bivalve mollusk, many other molluscan, as well as annelid and ascidian eggs, remain in metaphase until the sperm enters the egg or until the egg is stimulated to divide by artificial parthenogenesis (CONKLIN, 1917).

Meiosis, as it occurs in the American oyster, is of the typical type. It is uncertain just what is the cause or significance of the marked deviations from regular meiosis and fertilization sometimes observed.

As noted previously by GALTSOFF (1964), the time it takes for *C. virginica* eggs to be fertilized and to reach different stages of meiosis varies somewhat. This variation must depend on the maturity of the gametes, environmental factors, and genetic constitution of the eggs.

GALTSOFF (1964) earlier reported that polyspermy can occur in *C. virginica* eggs. Polyspermy was reported to be a common cause of abnormal development in the clam, *Cumingia*, also a bivalve mollusk (of the mud and sand dwelling Semelidae) when fertilization was delayed or when eggs received undue handling (MORGAN, 1910).

In more typical cases of female meiosis the first polar body divides while the second one is being formed, but exceptions are frequent. The second polar body rarely divides (CONKLIN, 1917). That the behavior of the two polar body nuclei in the American oyster should be rather unpredictable is not unexpected. In *Loligo*, a cephalopod mollusk, the first polar body divides more than once, whereas in other mollusks the polar body never divides (RAVEN, 1958).

EXPERIMENTAL GENETICS AND CELL BIOLOGY OF THE OYSTER EGG

The facility with which every later stage of female meiosis and fertilization can be followed in the oyster, is of much value in breeding studies and further makes these molluscan eggs excellent material for experimental studies on genetics and cell biology.

Parthenogenesis, with and without polar bodies, has been induced in several bivalves ; — in *Ostrea gigas*, the Japanese oyster (INABA, 1936); in *Cumingia* (MORRIS, 1917); in the boring clams, *Barnea* (RAVEN, 1958); and in *Caecella*, also a lamellibranch (RAVEN, 1958). Sporadic or induced parthenogenesis in the American oyster might well be of much practical use in selective breeding of oysters, as it has been in the production of homozygous, diploid stocks of maize (CHASE, 1964).

Formation of polar body nuclei is of particular significance, then, as a means of estimating the frequency of natural parthenogenesis in different American oyster stocks, and as an indicator of the success of attempts at inducing parthenogenesis.

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SUMMARY

Meiosis and fertilization in spawned eggs of the American oyster, *Crassostrea virginica,* are of the normal type found in the large majority of the metazoa and higher plants. Various deviations from the regular sequence of these events were not infrequent, however, in oyster eggs examined in this study. Meiosis and fertilization can be cytogenetically followed critically in these eggs, which, consequently, offer many opportunities for experimental manipulation of the genetic material.

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REMOVAL OF YOLK FROM OYSTER EGGS BY SOXHLET EXTRACTION FOR CLEAR CHROMOSOME PREPARATIONS

A. CROSBY LONGWELL and S. S. STILES, *U. S. Bureau of Commercial Fisheries, Biological Laboratory, Milford, Connecticut 06460*

ABSTRACT. **The mature, spawned eggs of the American Eastern oyster, *Crassostrea virginica* Gmelin, contain yolk which interferes with the preparation of chromosomes and nuclear groups for the study of meiosis, fertilization, and karyology. Most samples of eggs cannot be studied cytogenetically until the yolk is extracted. Simple and complete removal of all interfering yolky material can be efficiently accomplished, after Carnoy fixation in 3:1 alcohol-acetic acid, by extraction for 2 hr in a micro-Soxhlet apparatus with 1:1 mixture of chloroform and methyl alcohol. Standard orcein squashes can then be routinely made of these eggs hitherto considered refractory to clear staining of chromosomes. A thimble with a fritted glass end, pore size 40 μ, is used as a receptacle for the eggs in the Soxhlet apparatus. After extraction the eggs can readily be washed off the fritted glass with the aceto-orcein staining solution. If the eggs are to be stored for some time prior to squashing and staining, 45–60% acetic acid or Carnoy's alcohol-acetic acid 3:1 can be used for the storage fluid.**

Several aspects of our genetics program on the commercial American Eastern oyster, *Crassostrea virginica* Gmelin, necessitate the examination of chromosomes and of nuclear divisions of mature, spawned eggs during meiosis, fertilization, and cleavage. In the course of making cytogenetic preparations over the period from spring 1966 to spring 1967, it became obvious that the oysters maintained for year-round conditioning in the laboratory (Loosanoff and Davis 1963) were showing seasonal and some individual variations in the amount of stored material contained in their mature spawned eggs. In the fall and winter months, when the eggs were most heavily laden with yolk, only an occasional clear egg was analyzable microscopically. Extensive cytogenetic studies of such eggs are neither feasible nor reliable. During the remainder of the year the yolk content varied, depending on the individual oyster. Under almost any conditions, however, the yolk content was sufficient to emphasize the need for effective yolk removal. It is well documented that the glycogen content of oysters undergoes seasonal changes which are related to the development of gonads and spawning (Galtsoff 1964). In general, eggs of Lamellibranchiata are poor in yolk, especially proteid yolk, but they are noted for their high fat content (Needham 1942; Worley 1944; Raven 1958). Neither the ethyl alcohol nor acetic acid commonly used for fixation of material dissolves lipid and glycogen yolk—ethanol precipitates glycogen (Baker 1963).

Although the yolk particles show less in bright-field illumination than in phase contrast, the yolky material is so dense that the nuclear groups and chromosomes are obscured by it, even when they are specifically stained. The poor stainability of the chromosomes in oyster eggs by the Feulgen procedure, and by orcein or carmine necessitates, for routine cytogenetic analysis, the use of phase contrast in addition to staining. Other workers also have found phase contrast necessary in conjunction with staining for examination of chromosomes in eggs of two species of clams, also bivalve mollusks like the oyster (Menzel and Menzel 1965). Since the yolk globules and background cytoplasm of oyster eggs stain only to a very negligible extent with either aceto-orcein or aceto-carmine, prestaining hydrolysis with HCl improves the preparations only slightly by reducing stainability of this interfering material.

The yolk droplets and globules of oyster eggs do not appear to diminish in quantity during early cleavage, and this material is present in the same degree and form at all stages of fertilization and meiosis in the spawned eggs. Yolk particles of varying sizes may be distributed either throughout the fixed egg or massed in one large group occupying a considerable part of the total volume of the egg; therefore, it is not possible to circumvent yolk interference by restricting cytological analyses to any particular phase of meiosis or of early cleavage.

This report describes a simple, efficient method for complete extraction of lipid yolk from mature eggs of the American oyster intended for cytogenetic study.

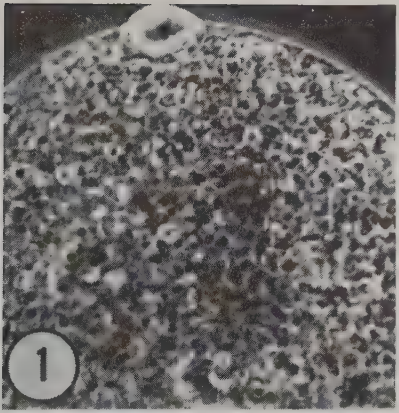
Biological Materials

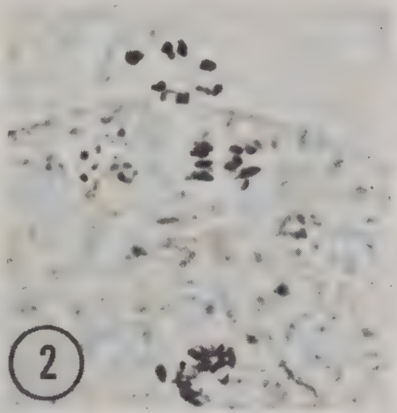
The spawned eggs and the sperm used in the laboratory fertilization of the *Crassostrea virginica* eggs were obtained from laboratory-conditioned wild oysters induced to spawn by thermal stimulation (Loosanoff and Davis 1963). These oysters were taken from the vicinity of the harbor of New Haven, Connecticut.

Extraction Methods

During the spring and summer months of 1966 the American oyster eggs could sometimes be reasonably well prepared for chromosome analysis and other nuclear cytological study by the usual fixation in Carnoy's alcohol-acetic 3:1 fluid and squashing in 1–2% orcein or carmine in 45–60% acetic acid without further prestaining treatment. With this simple procedure, special attention had to be given to time of fixation and other details that facilitated squashing the cells and spreading of the yolk particles over a large area. Often, however, in the months when the eggs contained much yolk, a cytogenetic study was impossible. In some samples, much of the yolk could be removed by stirring or shaking batches of the eggs in acetone, in a 1:1 chloroform-methyl alcohol mixture, or in chloroform. Acetone has the disadvantage of hardening the cells more rapidly than the other solvents.

In the fall and winter months, however, when the eggs were most heavily laden with yolk (figure 1) this extraction at room temperature did not sufficiently clarify them to make cytogenetic analyses possible even when extraction time was extended to several hours, or even days, and with several changes of relatively large volumes of the solvent. Prolonged heating of the solvents, with a sufficient number of changes of fresh solvent to simulate the





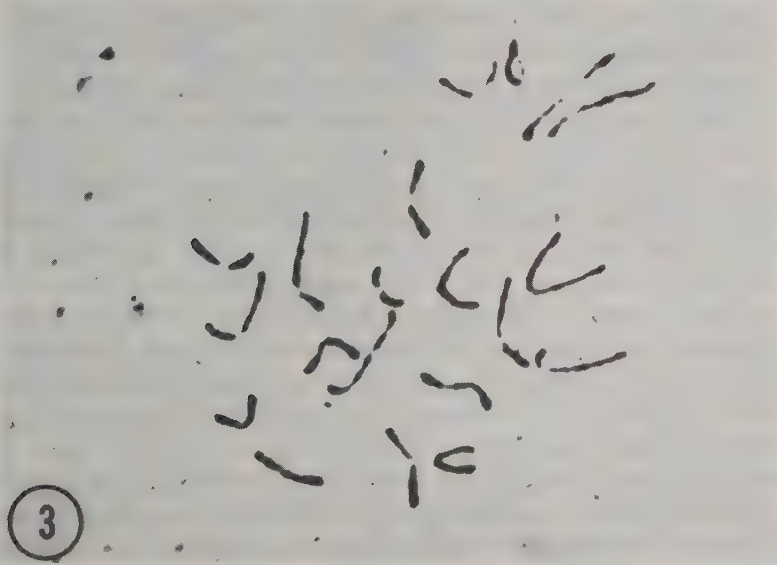


FIG. 1. Portion of a slightly squashed egg of the American oyster at early cleavage with polar bodies showing as a light region projecting from the egg at the top of the photomicrograph. Division groups are entirely obscured by yolk material. The photomicrograph has been printed to demonstrate the density of the yolk bodies. 100x phase-contrast objective, orcein stain. × 875

FIG. 2. Portion of a lightly squashed egg of the American oyster after Soxhlet extraction of the yolk. This egg is at an early cleavage stage comparable to that in Fig. 1. Cleavage division figures are now discernible against a clear cytoplasmic background. The polar body nucleus clearly shows individual metaphase chromosomes. 100x phase-contrast objective, orcein stain. × 1000

FIG. 3. The 20 chromosomes of an early cleavage metaphase of the American oyster after Soxhlet extraction. 100x phase-contrast objective, orcein squash. × 1750

conditions of Soxhlet extraction (described below), was found to be impractical. When eggs were checked microscopically at intervals during the extractions, it was found that little to no extraction of the yolk was occurring.

Preparations made by fixation in methyl alcohol-acetic acid, 1:1, though still poor, were somewhat more free of yolk than those made in the usual ethanol-acetic mixture 3:1, or after treatment in 60% acetic acid, or with direct squashing in the aceto-orcein. Methanol as a component of the fixative seemed to harden the cells somewhat more than ethanol and was therefore less suitable.

Substitution of proprionic acid for acetic acid in the Carnoy fixative and in the staining solution did not give clearer preparations. Addition of chloroform to the fixing solution did not result in any significant extraction of yolk. The use of typical lipid solvents prior to fixation made the eggs unsuitable for squashing and subsequent cytogenetic study.

The extraction of lipids from yolk-laden eggs was simplified and made more effective by use of a micro-Soxhlet apparatus. Most of the paper thimbles commonly used for holding the material to be extracted have too large a pore size to retain individual, free cells as the oyster eggs, which may be as small as 60 μ. In place of the usual thimble, a cut-to-size, ordinary fritted glass, gas-dispersion tube, 15 x 50 mm, with a pore size of 40–60 μ was used. An apparatus with a flask holding 40 ml of solvent was adequate and the small thimble facilitated recovery of the small quantities of free cells involved.

Since a hot mixture of equal parts of chloroform and methanol has been used extensively for removal of all lipid (simple and derived, and the compound phospholipids and glycolipids) from tissues (Casselman 1962), this solvent combination was chosen for the oyster eggs. That these solvents have no damaging effects on tissue is implied by their extensive use in fixatives. The solvent mixture was heated to its boiling point by immersing the flask in a standard, thermostatically controlled laboratory water bath operated at about 90 C. Two hours were found to be a suitable extraction time for complete removal of the yolk.

After extraction, the eggs are easily removed from the porous-bottom glass tube by rinsing them out with small quantities of the aceto-orcein or aceto-carmine in which they are to be squashed, or in either the Carnoy fixative or 45–60% acetic acid if they are to be stored.

Chromosomes and division groups from such extracted samples regularly show very distinctly against a quite clear cytoplasm which is free from any globular materials. There is no discernible distortion of the chromosomes, of the nuclear groups, or of the division figures. The spreading quality of the cells, so important for making good chromosome squashes, is affected very little by the extraction (figures 2 and 3). By contrast, when the eggs are kept in lipid solvents for the longer periods needed for extraction at lower temperatures, a definite hardening of the cells occurs.

Our experience indicates that, after storage in alcohol-acetic acid, or even in 45–60% acetic acid for more than 3 days, Soxhlet-extracted eggs do become hardened somewhat, and are then more difficult to squash than nonextracted eggs after similar storage. This occurs even if there has been thorough rinsing of the eggs in 45–60% acetic acid. If very detailed chromosome analyses are to be made, extraction should be delayed until preparations can be completed on the same day.

Prior to Soxhlet treatment, fixation may be in a 1:1 mixture of methyl alcohol and glacial acetic acid, or the eggs may simply be placed in aqueous 60% acetic acid. Extraction may be faster when fixation is in the fixing fluid made with methyl alcohol, or after treatment in the 60% acetic acid alone. Chromosome squashes, though, seem to be better after a regular fixing in Carnoy's 3:1 fluid made with ethyl alcohol.

Possibly an extraction at a suitable solvent-temperature-time combination could be found that would give complete extraction; however, it is far more convenient to extract in a Soxhlet apparatus when prolonged heating of the solvents is required.

Discussion

The exact composition of the extracted yolky material in the mature *C. virginica* egg is not known, or the effects on the yolk of the fixatives used. The lipid content of these eggs may be bound either in a complex of different fats, with protein or with carbohydrates, or any combination of them. The extent of binding, as well as the total yolk content, probably varies according to season, stock, individual oyster, and age of the eggs; thus greater or lesser difficulties with non-Soxhlet extraction methods may be encountered. Although a sample of eggs of the European oyster, *Ostrea edulis,* contained far more yolk than was ever observed in eggs of *C. virginica,* extraction was easily accomplished at room temperature with chloroform.

In a short review on the chromosomes of the Osteichthyes, Roberts (1967) notes that in nonsalmonids with small eggs the blastomeres are removed from the yolk only with great difficulty and some yolk invariably accompanies the blastomere and interferes with staining. Simon (1964) extracted the yolk from fertilized eggs of salmonid fishes after Carnoy fixation by merely passing them through absolute acetone. The interfering yolky material of marine gastropods was suppressed by staining in diluted Gomori's chrome alum-hematoxylin following hydrolysis at room temperature in hydrochloric acid (Cather 1959). Both gastropods and salmonids have long been popular objects of cytological study, possibly because they do not present the methodologic difficulties that are encountered in the oyster. Menzel and Menzel (1965), in a report on two species of clams and their hybrids, noted that because of the dense cytoplasm, eggs were difficult to squash for photomicrography. Most likely, much of this cytoplasmic density is attributable to yolk material.

The technique reported for marine gastropods (Cather 1959) precludes squashing, which is essential for karyological study of the oyster chromosomes, and convenient for spreading the division and fusion groups of the meiotic, fertilized eggs. Possibly, some air-drying procedures for the chromosomes of the oyster might be developed which would facilitate their spreading. However, orcein staining, and squashing following Soxhlet extraction, now gives the most desirable and most controllable results.

Use of the Soxhlet apparatus for extraction of interfering substances in samples intended for cytological or chromosome analysis is not mentioned in commonly used books on chromosome methodology but was suggested by Lhotka (1955) for tissues in general. Soxhlet extraction has been used in some biochemical procedures on oyster eggs (Cleland 1947); to some extent in the making of preparations for histochemical studies (Casselman 1962); and for histological preparations (Thompson 1966).

Soxhlet extraction can eliminate tedious and unrewarding analysis caused by poor cytological preparations. Moreover, the possibility of so easily making good preparations of oyster eggs should stimulate further investigations on the pelecypod mollusks, a group almost entirely unexplored cytogenetically. Such extraction should also be applicable to other types of fatty eggs, cells, and tissues intended for cytogenetic study for which other means of extraction have proved unsatisfactory. Good results have also been obtained with the solid gonadal tissues of both male and female oysters, which also have considerable amounts of lipid materials.

Yolk-laden animal eggs have been disregarded generally, or considered poor material for cytogenetic studies from the standpoint of methodology. This attitude is unfortunate in view of the excellent experimental research possibilities that eggs, such as those of the American oyster, which might be obtained by the millions at each stage of meiosis, fertilization, and cleavage, offer to the cell biologist.

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QUANTITATIVE AND QUALITATIVE COMMENSAL BACTERIAL FLORA OF *CRASSOSTREA VIRGINICA* IN CHESAPEAKE BAY

T. E. Lovelace, H. Tubiash and R. R. Colwell
DEPARTMENT OF BIOLOGY, GEORGETOWN UNIVERSITY, WASHINGTON,
D. C., AND U. S. BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL
LABORATORY, OXFORD, MARYLAND

ABSTRACT

The natural commensal flora of the oyster has been under study since July, 1966. Two areas of Chesapeake Bay were selected for investigation: Marumsco Bar, where severe mortalities occur annually, and Eastern Bay, a productive commercial oyster harvesting area. Water, mud, oyster mantle fluid and oyster gill tissue were examined for quantitative and qualitative estimates of total viable aerobic heterotrophic bacteria. In general, the two areas of Chesapeake Bay which were sampled are very similar in pH, dissolved oxygen, seasonal temperature range and salinity. Little quantitative variation was observed between samples within each area and between areas. The water counts ran at approximately 4×10^{2}*/ml., the mud* 10^{4}*-*10^{5}*/ml, oyster gill tissue* 10^{3}*-*10^{4}*/gm and the mantle fluid* 5×10^{4}*/ml. Quantitatively, there was also little or no seasonal or environmental variation. From counts made on basal salts medium and on distilled water medium, salt-requiring bacteria appear to be a significant part of the bacterial flora of both areas. From the generic distribution of the bacterial types for the two areas tested, it was found that 81 per cent of the Marumsco Bar water, mud and animal samples consisted of* Vibrio, Pseudomonas *and* Achromobacter *spp., whereas the Eastern Bay representation of these genera was 46 per cent.* Cytophaga/Flavobacterium *spp. was the dominant group in the Eastern Bay samples. The Marumsco Bar area harbors significantly greater numbers of* Vibrio *spp. Overall the Eastern Bay area represents a "balanced" microbial population.*

INTRODUCTION

The natural commensal flora of marine invertebrate animals has not been studied to any great extent. There is some published work on bacteria isolated from shellfish but the focus has been chiefly on the public health aspects of the animals and their environment. In 1959 the natural flora of *Crassostrea gigas* was investigated (Colwell and Liston, 1960). The research effort was directed primarily to obtain information which would aid shellfisheries technologists in establishing handling methods for prevention of product spoilage. It was subsequently established that the natural flora of *C. gigas* is composed of organisms representing the genera *Pseudomonas*, *Achromobacter*, *Flavobacterium* and *Vibrio* (Colwell and Liston, 1960). Dead and dying oysters in populations of *C. gigas* grown in Hood Canal, Oyster Bay and Willapa Bay, Washington, included a somewhat greater incidence of *Pseudomonas* spp. (Colwell and Sparks, 1967).

Several investigators have induced pathological conditions in oysters (Tripp, 1960; Pauley and Sparks, 1965), or succeeded in producing bacterial infection (Feng, 1966). *Pseudomonas enalia*, a bacterial pathogen for *C. gigas*, was recently described by Colwell and Sparks (1967).

Since July, 1966, we have undertaken a study of the natural commensal flora of *Crassostrea virginica* in Chesapeake Bay. Two areas were selected for our investigation: Marumsco Bar, where severe mortalities occur annually, and Eastern Bay, a productive commercial oyster-harvesting area. The work has been undertaken to obtain information concerning the microbial ecology of *C. virginica* in its natural habitat and possible involvement of

TABLE 1. *Environmental parameters — Marumsco Bar and Eastern Bay.*

Location	Date	Temperature °C			pH		Salinity (ppt)		Dissolved Oxygen (ppm)*		Depth (ft)
		Air	Sur.	Bot.	Sur.	Bot.	Sur.	Bot.	Sur.	Bot.	
Marumsco Bar	8-15-66**	—	25.8	—	8.1	—	19.5	—	—	9.0	8-9
Marumsco Bar	8-29-66	—	26.8	—	8.2	—	18.8	—	—	—	10
Marumsco Bar	9-19-66	—	21.5	—	7.8	8.0	19.8	—	—	—	10
Marumsco Bar	10-13-66	19.5	17.8	17.8	—	—	—	—	—	—	10
Marumsco Bar	3-21-67	9.0	3.9	4.0	—	—	15.6	16.2	12.24	12.39	—
Eastern Bay	11-7-66	10.0	11.7	11.3	7.5	7.6	17.2	17.3	—	10.40	10
Eastern Bay	1-17-67	9.3	2.7	3.5	—	—	15.8	—	12.69	12.67	—
Eastern Bay	3- 2-67	7.7	1.0	—	—	—	—	—	14.48	14.24	—

*Winkler method, in ppm.

**Dockside salinity = 15-17 ppt, dissolved oxygen = 3.5 ppm, pH = 7.3.

the commensal bacteria in Chesapeake Bay oyster mortalities.

METHODS

Both areas of Chesapeake Bay, Marumsco Bar and Eastern Bay, were sampled every 6 weeks. In the study reported here, water and mud from each area were collected aseptically in sterile containers. Five oysters, randomly selected from a trawl, were collected and, with the water and mud, stored separately on ice during transport to the laboratory. Initially, all samples of mud, water and oysters were analyzed on the boat (immediately after collection) and again back at the laboratory to determine the effect of time lapse and cold storage on the bacterial flora. The time lapse from sampling to analysis in the laboratory was, on average, 4 to 6 hours.

The animal, water and mud samples were analyzed by serial dilution, using sterile water collected from the sampling stations as diluent, and enumeration of bacteria by the aerobic spread plate count technique. Bacterial counts were determined after 5 days' incubation of the inoculated plates at 25°C. The oysters were examined by first placing the animals on sterile paper, cleansing the shell exterior and then opening the shell with a shucking knife which had been sterilized by immersion in alcohol followed by flaming. A sterile pipette was used to withdraw 1.0 ml mantle fluid. A composite of gill tissue excised from each of 5 oysters was also examined bacteriologically. The gill tissue (0.2 gm from each animal) was pooled and homogenized in a mechanical blender for 1 minute.

From each count plate 30-40 colonies were selected at random and transferred to a basal medium consisting of: 0.3 per cent yeast extract (Difco), 1.0 per cent proteose peptone (Difco), 2.4 per cent NaCl, 0.07 per cent KCl, 0.53 per cent

TABLE 2. *Total viable aerobic heterotrophic bacterial populations from water, mud and animals of Marumsco Bar and Eastern Bay. Figures represent counts in replicate.*

Location	Date	Water	Mud	Gills*	Mantle Fluids*
Marumsco Bar	8-15-66	4.0×10^2	8.2×10^4	5.2×10^4	5.0×10^4
Marumsco Bar	8-29-66	4.5×10^2	1.0×10^5	3.0×10^4	5.0×10^4
Marumsco Bar	9-19-66	7.3×10^2	6.1×10^5	7.0×10^3	3.5×10^4
Marumsco Bar	10-13-66	2.5×10^2	7.0×10^4	6.1×10^4	4.8×10^4
Marumsco Bar	3 21-67	6.0×10^2	9.0×10^4	2.5×10^3	3.5×10^4
Eastern Bay	11- 7-66	4.0×10^3	9.0×10^5	8.0×10^4	2.6×10^5
Eastern Bay	1-17-67	1.1×10^2	8.8×10^5	1.5×10^3	9.2×10^4
Eastern Bay	3- 2-67	4.6×10^3	4.2×10^5	4.3×10^4	9.2×10^4

*Average of 5 individual oysters.

TABLE 3. *Comparison of shipboard and laboratory total viable counts. Figures from replicate counts.*

		Mud		Water		Mantle Fluid	
Location	Date	Shipboard	Laboratory	Shipboard	Laboratory	Shipboard	Laboratory
Marumsco Bar	9-19-66	8.6×10^5	6.1×10^5	6.5×10^2	7.3×10^2	7.2×10^3*	4.0×10^3
Eastern Bay	11-7-66	9.0×10^5	9.0×10^5	3.0×10^2	4.0×10^2	2.4×10^4	2.6×10^5

*Data for a single animal; other Mantle Fluid data are an average of 5 animals tested.

$MgCl_2$, 0.7 per cent $MgSO_4 \bullet 7H_2O$, 2.0 per cent agar (Difco), pH 7.2-7.4. After purification, the cultures were subjected to a battery of tests using methods previously described (Colwell, 1964; Moffett and Colwell, 1968; Quigley and Colwell, 1968; Colwell, 1968). The taxonomic data were coded and transferred to IBM cards for computer analysis following the method of Colwell and Liston (1961b). Computer analyses were carried out on the IBM 1620 computer using Georgetown Taxonomy (GTP) programs GTP-2, GTP-4 and GTP-5.

RESULTS AND DISCUSSION

Selected parameters describing the areas of Chesapeake Bay under survey are presented in Table 1. A seasonal drop in temperature, accompanied by slight salinity changes, occurred. The temperature range for both areas was roughly 1-25°C and salinity *ca.* 15-20 ppt. Dissolved oxygen content ranged from 9 to 15 ppm.

Total viable aerobic heterotrophic bacterial populations from mud, water and animal samples taken from the two areas under study are listed in Table 2. A striking observation was the lack of fluctuation in the quantitative data. The total viable counts were found to be: water sample 4×10^2/ml; mud 10^4-10^5/ml; oyster gill tissue 10^3-10^4/gm, and mantle fluid 5×10^4/ml. Quantitatively there was, therefore, no seasonal or environmental variation.

Because it was possible that laboratory counts were not reflecting the natural situation, several bacteriological analyses were performed on the boat immediately upon sampling. No significant differences between shipboard counts and laboratory counts could be detected (Table 3). The counts obtained were well within statistical error expected for the bacteriological counting procedure.

A comparison of media for counts was also done. It is considered easier and more precise to use a synthetic medium, that is, in terms of ease

TABLE 4. *Comparison of media used in total viable counts of samples from Marumsco Bar (M. B.) and Eastern Bay (E. B.) areas.*

		Mud $\times 10^4$/ml			Water $\times 10^2$/ml			Gill Tissue $\times 10^3$/g			Mantle Fluid* $\times 10^3$/ml		
			ye-4			ye-4			ye-4			ye-4	
Area **	Date	Area[1]	salts[2]	yens[3]	Area	salts	yens	Area	salts	yens	Area	salts	yens
M.B.	10-13-66	7	16	2.8	2.5	2.2	0.3	61	50	6.5	48	41	0.6
E.B.	11- 7-66	90	100	1.2	3	2	0.3	80	45	3.5	260	25	4.7
E.B.	1-17-67	88	—	11	1	—	0.8	1.5	—	$<10^3$	92	—	33
E.B.	3- 2-67	42	—	14	4.6	—	1.8	43	—	2	92	—	7
M.B.	3-21-67	9	—	7	6	—	0.9	2.5	—	0.5	35	—	3.9

*Pooled data. Each figure represents an average of 5 animals tested.

**Samples plated on board collecting vessel.

(1) Water from the sampling areas as diluent.

(2) Yeast extract (Difco) 0.3%, Proteose peptone (Difco) 1.0%.
NaCl 2.4%
KCl 0.07%
$MgCl_2$ 0.53%
$MgSO_4$ 0.7%
pH 7.2-7.4

(3) Yeast extract (Difco) 0.3%, Proteose peptone (Difco) 1.0%, distilled water, pH 7.2-7.4 (Tris buffer).

TABLE 5. *Generic distribution of bacterial types in samples tested.**

Taxonomic Group	Marumsco Bay	Eastern Bay
Vibrio spp.	46%	20%
Pseudomonas spp.	22%	9%
Achromobacter spp.	13%	17%
Corynebacterium spp.	5%	7%
Cytophaga/Flavobacterium spp.	3%	30%
Micrococcus/Bacillus spp.	0%	6%
Enterics**	7%	3%
Other***	3%	8%
Total isolates in sample	125	104

*Total number of strains studied = 229

**Enterics: *Enterobacter* spp., *Proteus* spp.

***Other: *Caulobacter* spp., *Saprospira* spp., *Spirillum* spp.

of preparation, duplication of experiments, assembly of materials, etc. We attempted to simulate the salts of the environment in the medium by employing a Na^+, K^+ and Mg^{++} mineral supplement. From the data presented in Table 4, two points are clear. First, the counts on the distilled water-based medium were at least an order of magnitude lower than the counts on the medium prepared with water from the sampling areas or a salts base as diluent. Second, the medium prepared with a salts basal supplement did not always equal the medium prepared with area water as diluent in terms of total viable counts but better approximated the area water counts than did the distilled waterbased medium. Thus, a requirement for the cations, Na^+, K^+ or Mg^{++} (which constitute the basal salts supplement), was indicated for a significant portion of the aerobic hetero-

TABLE 6. *Generic distribution of bacterial types by area and month of sampling.*

		Taxonomic Groups*							
Date	Location	*Vibrio* spp.	*Pseudomonas* spp.	*Achromobacter* spp.	*Corynebacterium* spp.	*Cytophaga/Flavobacterium* spp.	*Micrococcus/Bacillus* spp.	Enterics**	Other***
June, 1966	Marumsco Bar	57%	24%	4.7%	0	9%	0	0	4.7%
Aug., 1966	Marumsco Bar	30%	33%	18%	12%	0	0	6%	0
Aug., 1966	Marumsco Bar	30%	27%	11%	4%	8%	0	19%	0
Sept., 1966	Marumsco Bar	58%	17%	13%	5%	0	0	8%	0
Oct., 1966	Marumsco Bar	66%	5%	14%	0	0	0	0	14%
Nov., 1966	Eastern Bay	20%	9%	17%	7%	30%	6%	3%	8%
Jan., 1967	Eastern Bay	19%	5%	19%	3%	38%	11%	0	3%
Mar., 1967	Eastern Bay	17%	6%	17%	14%	14%	5%	8.5%	20%

*Total number cultures studied = 229

**Enterics: *Enterobacter* spp., *Proteus* spp.

***Other: *Caulobacter* spp., *Saprospira* spp., *Spirillum* spp.

TABLE 7. *Generic distribution of bacterial types in the mud, water and animal samples.**

	Mud		Water		Animals	
Taxonomic Group	Marumsco Bar	Eastern Bay	Marumsco Bar	Eastern Bay	Marumsco Bar	Eastern Bay
Vibrio spp.	37%	22%	56%	17%	47%	21%
Pseudomonas spp.	10%	11%	18%	0	27%	9.5%
Achromobacter spp.	16%	6%	13%	42%	11%	16%
Corynebacterium spp.	26%	22%	0	0	1%	4%
Cytophaga/Flavobacterium spp.	0	38%	6%	8%	3%	32%
Micrococcus/Bacillus spp.	0	0	0	0	0	8%
Enterics**	10%	0	6%	25%	7%	0
Other***	0	0	0	8%	4%	9.5%
Total in sample	19	18	16	12	90	73

*Total sample studied = 229

**Enterics: *Enterobacter* spp., *Proteus* spp.

***Other: *Caulobacter* spp., *Saprospira* spp., *Spirillum* spp.

trophic bacterial flora.

Since no significant differences were detected in quantitative distribution of the bacteria by season or by area, the qualitative distribution of bacterial types was examined. The generic distribution of bacteral types for each of the two areas is listed in Table 5. A very real difference in the types of bacteria isolated was noted. In the Marumsco Bar area, there was a much greater incidence of *Vibrio* and *Pseudomonas* spp. than *Cytophaga/Flavobacterium* spp. The *Achromobacter* and other groups were an approximately equal portion of the flora in both areas. The significance of this observation is enhanced when it is pointed out that the *Vibrio* and *Pseudomonas* spp. isolated were, in general, very active in their metabolic capacities, being lipolytic, proteolytic and saccharolytic.

Further examination of the qualitative distribution of the bacterial groups by season was carried out (Table 6). An indication of some fluctuation was noted for the Marumsco Bar area. *Vibrio* and *Pseudomonas* spp. appeared to be somewhat even more dominant in late spring and early autumn.

Finally, a breakdown of bacterial types by mud, water and animal was made (Table 7). In Marumsco Bar, the *Vibrio* and *Pseudomonas* spp. were dominant in all samples taken, especially in water and animal samples.

It is noteworthy that the results of the Chesapeake Bay study are in general agreement with the results of a similar study undertaken on the West Coast (Colwell and Liston, 1960; 1961a). The Eastern Bay data (Table 5) approximate the results obtained for Hood Canal, Willapa Harbor and Oyster Bay in Washington State. A notable exception is the high incidence of *Vibrio* and *Pseudomonas* spp. found in Marumsco Bar, Chesapeake Bay, which was not observed in any of the areas of Washington that were examined.

The quantitative data compare favorably with the results of Colwell and Liston (1960), since 10^4-10^5 organisms per ml oyster liquid was observed both for the West Coast animals and those of Chesapeake Bay (see Table 2).

CONCLUSIONS

The two areas of Chesapeake Bay which were investigated in this study show no significant quantitative difference in the natural bacterial flora of *Crassostrea virginica*. A relatively constant total viable population of bacteria was found in the Chesapeake Bay mud and water and on the animals. The quantitative estimates of the total viable aerobic heterotrophic bacterial populations for these samples were nearly identical to results obtained in a similar study of animals on the Pacific Coast, undertaken in 1959-1961.

The qualitative composition of the flora of the samples taken in the two areas of Chesapeake Bay, however, was markedly different. The Marumsco Bar area harbors significantly greater numbers of *Vibrio* spp. The Eastern Bay area, on the other hand, was similar to the Pacific Coast areas sampled, demonstrating a "balanced natural flora." Infection studies with the *Vibrio* spp. are now underway in the hope that their involvement in, or contribution to, the disease condition prevalent in Marumsco Bar, can be determined.

and it seems worthwhile to see how it would serve in examining the deep and bottom waters of the world ocean.

In examining the field of potential density in the world ocean we found that it has a very peculiar distribution in the western Atlantic, and in the process of trying to understand this distribution we have been led to consider different methods of dealing with deep flow and mixing.

ABYSSAL CHARACTERISTICS

Salinity, potential temperature and potential density values are shown in Figs. 1–3 for the bottom or near-bottom waters of the world ocean. (Stations are identified in Table 1.) The purpose is to represent the deepest water found in the basins and the trend of its characteristics. No attempt is made to show detail: only the typical values in the major ocean basins are shown. The values shown do not represent values at a common depth but were taken as near to the bottom as possible in deep water.

The shallowest value shown is not in a basin; rather it is in the Denmark Straits. All other values are found at depths exceeding 2900 m. In some regions, such as the northern North Pacific, the vertical and horizontal gradients near the bottom are relatively weak and the values given for the three quantities are representative of large areas. In other regions, such as the western South Atlantic, there is more variation and the values given represent extremes.

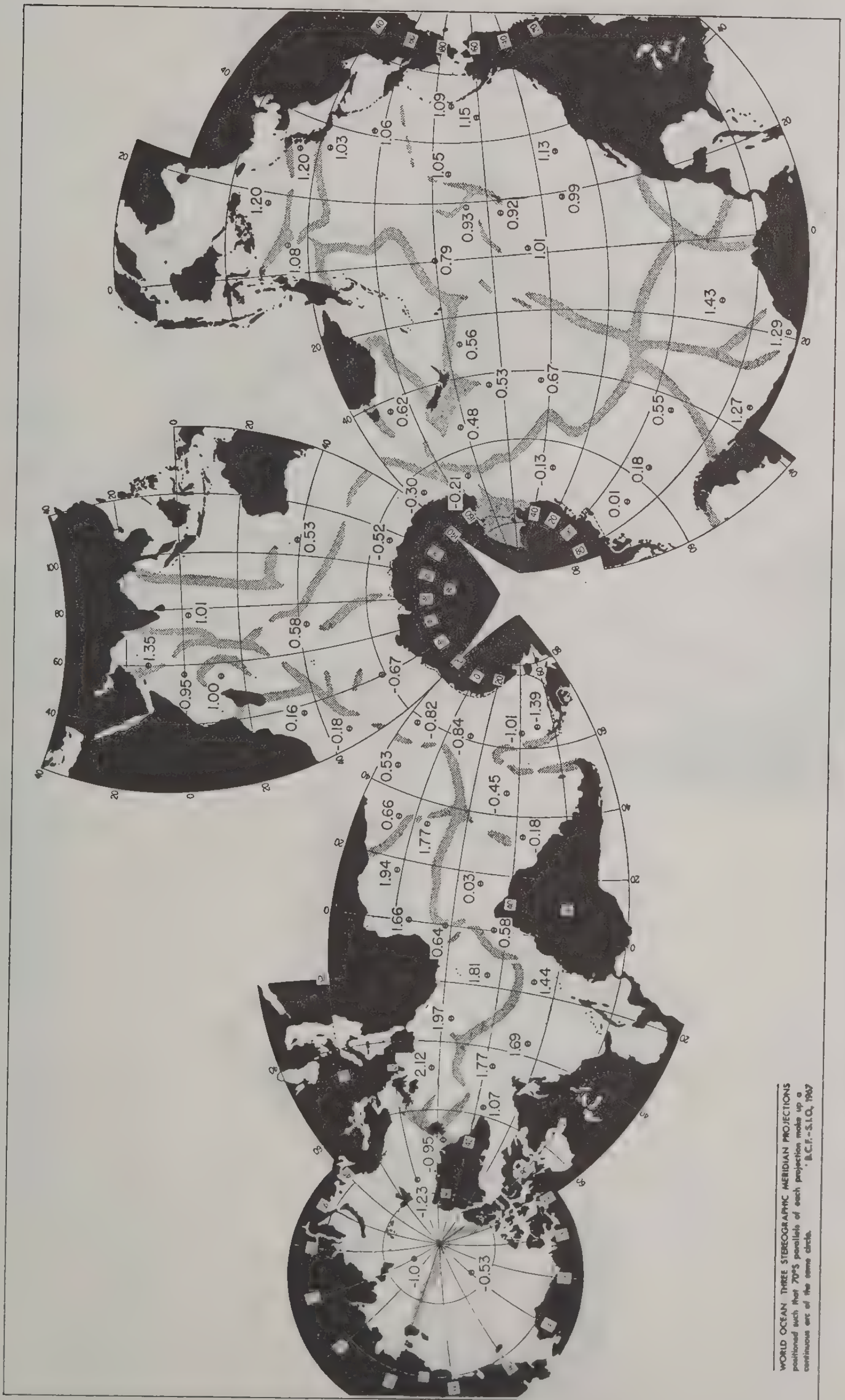
The major ridges which separate the principal ocean basins are indicated roughly by areas of stippled shading; this shading does not represent a common depth interval.

Potential temperature

The potential temperature is the temperature a water sample would have if raised adiabatically to the sea surface (these values were calculated from the expression prepared by FOFONOFF, 1962). Potential temperature (Fig. 1) is as low as − 1·23°C in the Norwegian and Arctic seas: the highest for a deep major basin (2·12°C) is in the adjacent eastern North Atlantic. The lowest potential temperature (− 1·39°C at 2921 m, *Eltanin* Sta. 262) is found in the western side of the deep basin adjacent to the Weddell Sea shelf. Two other extreme values (below − 1·30°C) were recorded in that region during the same expedition (*Eltanin* Cruise 12, Stas. 261 and 263). The water with this extreme characteristic appears to be a thin stratum extending over a very limited region. Typical values for the deepest parts of this basin range between − 0·90 and − 1·00°C (GORDON, 1966). Eastward from the Weddell Sea the potential temperature increases gradually around Antarctica to about 0·01°C in the Pacific Antarctic. Northward from Antarctica the potential temperature increases in the Indian Ocean (to 1·35°C), in the open North Pacific (to 1·15°C), and in the eastern Atlantic (to 2·12°C). In the western Atlantic there is an increase to a maximum of 1·77°C near 45°N followed by a decrease. The position of this maximum may indicate the northern limit of the direct influence of Antarctic Bottom Water and the southern limit of the bottom water formed from Norwegian–Greenland Sea overflow.

Salinity

Salinity (Fig. 2) is highest (34·977‰) in the Alaskan basin of the Arctic Sea. The deep water of this basin is cut off from the rest of the Arctic Sea at about 2300 m


WORLD OCEAN THREE STEREOGRAPHIC MERIDIAN PROJECTIONS positioned such that 70°S parallels of each projection make up a continuous arc of the same circle.
B.C.F.–S.I.O. 1967
1.20
1.20
1.03
1.06
1.09
1.15
1.05
1.13
0.99
0.92
0.93
0.79
1.08
1.01
1.43
1.29
0.56
0.53
0.67
0.62
0.48
0.55
1.27
-0.30
-0.21
-0.13
0.18
0.01
0.53
-0.52
1.01
1.35
0.58
0.95
1.00
-0.67
0.16
-0.18
-0.82
-0.84
-1.01
-1.39
0.53
0.66
1.77
-0.45
-0.18
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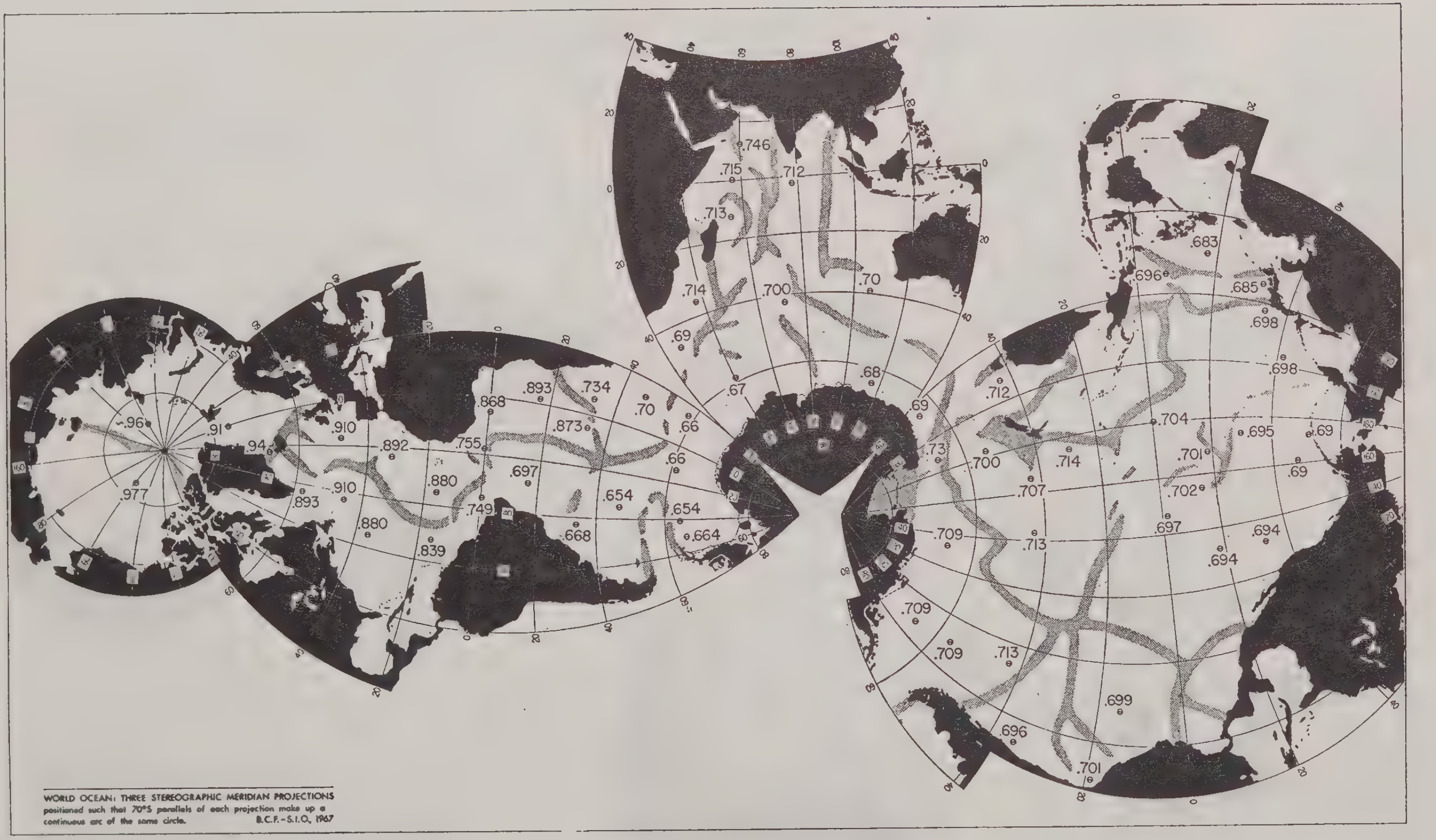
0.03
1.66
0.64
0.58
1.81
1.44
1.97
2.12
1.77
1.69
1.07
-0.95
-1.23
-1.0
-0.53

Fig. 1. Potential temperature (°C) at abyssal depths in the world ocean. Darkened areas represent the major elevations separating the principal basins.


.96
.977
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.892
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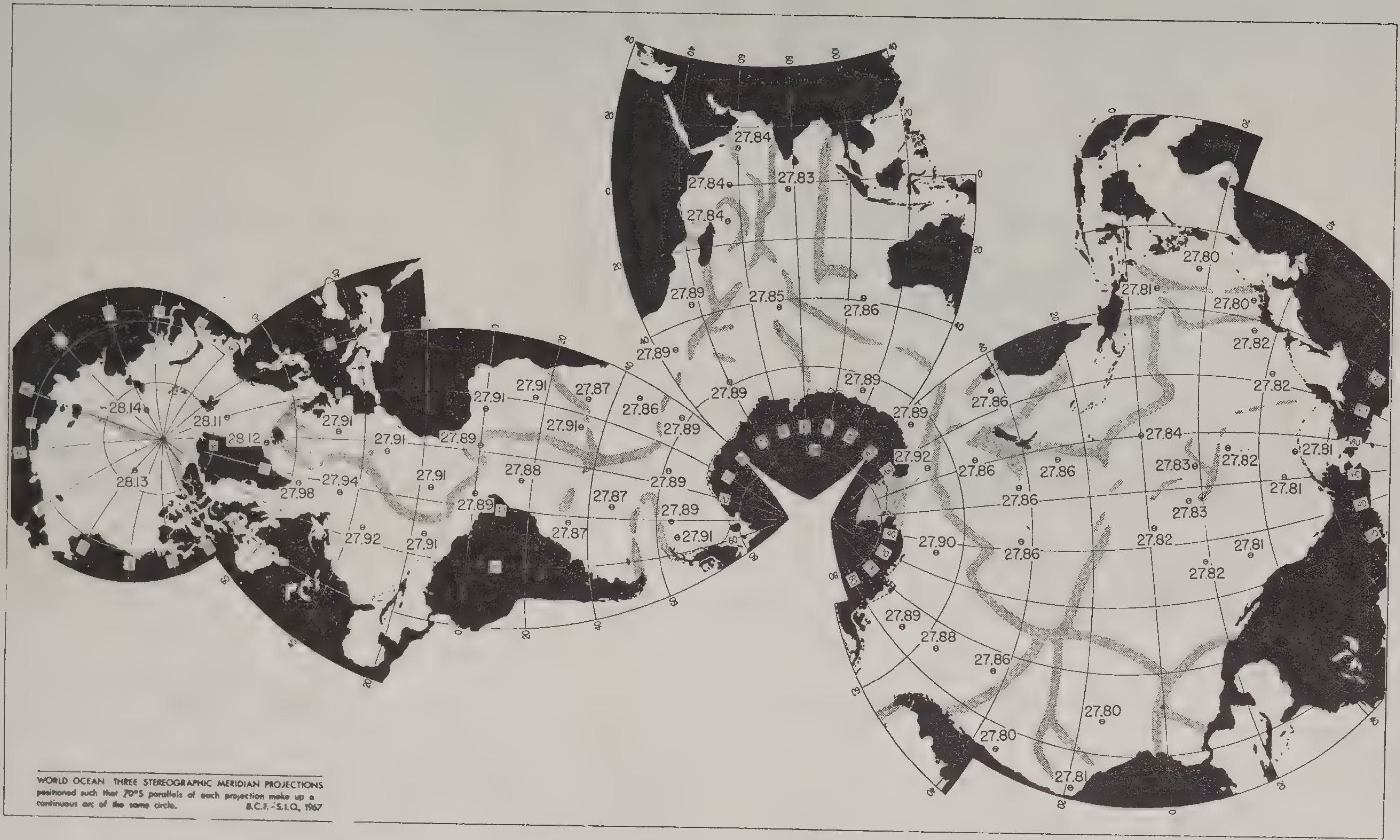
WORLD OCEAN: THREE STEREOGRAPHIC MERIDIAN PROJECTIONS
positioned such that 70°S parallels of each projection make up a
continuous arc of the same circle.
B.C.F.-S.I.O., 1967

Fig. 2. Salinity (‰) at abyssal depths in the world ocean. All values should have 34 added. Three-digit numbers indicate measurements by salinometer. Two-digit numbers indicate measurements by titration or salinometer measurements reported to two digits.


WORLD OCEAN THREE STEREOGRAPHIC MERIDIAN PROJECTIONS positioned such that 70°S parallels of each projection make up a continuous arc of the same circle. B.C.F.–S.I.O., 1967
28.14
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27.82
27.80
27.81

Fig. 3. Potential density (σ_θ) at abyssal depths in the world ocean. Units are grams per liter.

Table 1. Stations used on the maps of abyssal characteristics (listed south to north).

Ship or expedition	*Station*	*Lat.*	*Long.*	*Date*	*Data source*
		A. Atlantic and Arctic Oceans			
Eltanin Cr. 12	262	64° 55′S	52° 10′W	17 III 64	Jacobs (1965)
	266	64° 00′S	40° 50′W	21 III 64	
Discovery II	1146	61° 00′S	12° 04′W	6 III 33	Discovery Committee (1942)
	1158	58° 37′S	14° 43′E	16 III 33	
Eltanin Cr. 9	170	46° 50′S	35° 05′W	19 VIII 63	Jacobs (1965)
Discovery II	1162	46° 47′S	12° 39′E	21 III 33	Disc. Comm (1942)
Atlantis Cr. 247	5842	32° 31′S	5° 14′E	2 VI 59	Fuglister (1960)
	5810	32° 29′S	42° 50′W	28 IV 59	
	5829	32° 27′S	5° 19′W	13 V 59	
Crawford Cr. 10	128	15° 43′S	29° 17′W	4 IV 57	Fuglister (1960)
	146	15° 44′S	1° 50′E	18 IV 57	
Cr. 22	472	0° 15′S	5° 42′W	11 XI 58	
	495	0° 15′S	35° 01′W	27 XI 58	
	482	0° 09′S	18° 08′W	21 XI 58	
Cr. 16	302	16° 14′N	51° 58′W	25 XI 57	
	290	16° 15′N	35° 23′W	19 XI 57	Fuglister (1960)
Discovery II Cr. 2	3640	32° 13′N	23° 32′W	1 XII 57	Fuglister (1960)
Chain Cr. 7	43	36° 14′N	55° 10′W	26 IV 59	Fuglister (1960)
Discovery II Cr. 1	3520	45° 17′N	43° 37′W	18 IV 57	Fuglister (1960)
	3539	48° 34′N	16° 44′W	25 IV 57	
Erika Dan	316	57° 26′N	43° 56′W	29 III 62	Woods Hole Oceanogr. Inst. MS data NODC 31170
Anton Dohrn	1595	67° 33′N	24° 14′W	2 IV 57	Cons. Perm. Internat. Explor. Mer (1964)
G. O. Sars	185	76° 18′N	2° 00′W	25 IV 58	Cons. Perm. Internat. Explor. Mer (1965b)
Ice Island T-3	1	82° 42′N	158° 16′W	12 VIII 63	Lamont Geol. Obs. MS data, NODC 31483
(*Arctic*)	—	Eurasian basin			Sverdrup (1956) Timofeyev (1957)
		B. Indian Ocean			
Discovery II	2168	63° 29′S	115° 27′E	10 I 38	Disc. Comm. (1947)
	852	58° 40′S	40° 04′E	17 IV 32	Disc. Comm. (1942)
	848	45° 48′S	27° 14′E	12 IV 32	
Argo (Monsoon)	IV-11	42° 04′S	70° 40′E	21 XII 60	Scripps Inst. Oceanogr. MS data
Discovery II	2147	39° 21′S	106° 00′E	14 XII 37	Disc. Comm. (1947)
Anton Bruun Cr. 7	384	35° 44′S	36° 47′E	2 IX 64	Woods Hole Oceanogr. Inst. (1965b)
Argo (Dodo)	86	12° 00′S	55° 55′E	5 IX 64	Scripps Inst. Oceanogr. MS data
Argo (Lusiad)	II-72	0° 56′S	79° 03′E	2 IX 62	Scripps Inst. Oceanogr. MS data
	II-21	0° 01′N	57° 05′E	17 VII 62	
Anton Bruun Cr. 4A	180	12° 15′N	59° 42′E	20 X 63	Woods Hole Oceanogr. Inst. (1965a)

Table 1—(contd.)

Ship or expedition	*Station*	*Lat.*	*Long.*	*Date*	*Data source*
			C. Pacific Ocean		
Discovery II	1669	66° 04′S	172° 23′E	1 II 36	Disc. Comm. (1947)
Eltanin Cr. 17	414	66° 00′S	134° 56′W	3 IV 65	Jacobs (1966)
Discovery II	1699	64° 60′S	145° 49′E	15 III 36	Disc. Comm. (1947)
Eltanin Cr. 11	255	64° 57′S	87° 00′W	29 I 64	Jacobs (1965)
Cr. 13	293	56° 05′S	90° 17′W	20 V 64	
Argo (Monsoon)	VI–25	54° 10′S	177° 29′W	17 II 61	Scripps Inst. Oceanogr. MS data
Scorpio	43	43° 15′S	143° 43′W	13 IV 67	Scripps Inst. Oceanogr.—Woods Hole Oceanogr. Inst. MS data
	6	43° 15′S	152° 07′E	14 III 67	
	65	43° 14′S	93° 24′W	1 V 67	
	33	43° 12′S	166° 47′W	5 IV 67	
	83	35° 16′S	74° 08′W	15 V 67	
	149	28° 15′S	175° 49′W	13 VIII 67	
Horizon (Step-I)	47	19° 09′S	71° 58′W	10 XI 60	Scripps Inst. Oceanogr. (1961)
	16	15° 40′S	87° 58′W	14 X 60	
Argo (Monsoon)	N	0° 14′N	179° 59′E	25 IX 60	Scripps Inst. Oceanogr. MS data
	VIII-11	2° 00′N	147° 06′W	2 IV 64	
Spencer F. Baird (Proa)	H-14	7° 44′N	134° 56′E	23 IV 62	Scripps Inst. Oceanogr. (1966b)
Spencer F. Baird (Tethys)	C-56	14° 12′N	155° 08′W	29 VII 60	Scripps Inst. Oceanogr. MS data
Takuyo	66130	17° 01′N	128° 57′E	5 IX 66	Marit. Saf. Agency (1967)
Argo (Monsoon)	VIII-29	18° 07′N	133° 12′W	12 IV 61	Scripps Inst. Oceanogr. MS data
Horizon (Spheres)	1	18° 45′N	168° 31′W	6 IX 66	Scripps Inst. Oceanogr. MS data
Argo (Zetes V)	H-1	29° 36′N	174° 14′W	17 VI 66	Scripps Inst. Oceanogr. (1966a)
Atlantis II	853	31° 54′N	134° 26′E	4 IX 65	Woods Hole Oceanogr. Inst. (1966)
Alexander Agassiz (CCOFI 6304)	60.180	33° 37′N	132° 06′W	26 IV 63	Scripps Inst. Oceanogr. (1964)
Atlantis II	879	34° 08′N	143° 11′W	19 IX 65	Woods Hole Oceanogr. Inst. (1966)
Argo (Boreas)	167	41° 46′N	156° 47′E	18 III 66	Scripps Inst. Oceanogr. (1966a)

by the Lomonosov ridge. A salinity of about 34·96‰ has been estimated for the European basin (Timofeyev, 1957). A salinity of 34·91‰ is found in the Norwegian and Greenland basins and south of the Greenland–Iceland ridge. Salinity is lowest (34·654‰) in the Weddell Sea, increasing eastward around Antarctica (to 34·709‰ in the Pacific Antarctic Basin). There is a high value of 34·73‰ near the Ross Sea with a potential temperature of − 0·21°C (2960 m): this water must originate in the Ross Sea. From the Antarctic salinity increases northward in the Atlantic (to 34·91‰ at 45°N), in the northwestern Indian Ocean (to 34·746‰), and in the Pacific Ocean to a maximum (of about 34·714‰) near 30°S, then decreases (to about 34·69‰) in the open North Pacific.

Potential density

Potential density (ρ_θ) is the density a parcel of water would attain if raised abiabatically to the sea surface (where pressure is assumed to be one atmosphere). We will use the conventional abbreviation $\sigma_\theta = 10^3 (\rho_\theta - 1)$ where σ_θ is expressed in g/l. Potential density (Fig. 3) is highest in the Arctic Ocean and Norwegian Sea where ρ_θ is 1·02811–1·02814 g/ml and σ_θ is 28·11–28·14 g/l. Values of σ_θ south of Iceland are all less than 28 g/l. There is a secondary high (27·91 g/l.) in the Weddell Sea. The values decrease (to 27·89 g/l.) in this basin and then remain almost constant around Antarctica except for the value (27·92 g/l.) at the station near the Ross Sea, which was mentioned before. Values decrease northward from Antarctica through the Indian Ocean (to 27·83 g/l.), the Pacific Ocean (27·82 or 27·80 g/l.), but increase northward in the Atlantic Ocean (to 27·98 g/l. south of Greenland and to more than 28 g/l. in the Norwegian and Greenland seas).

Bottom waters have not been compared this way before, but the results are consonant in most cases with the ordinary concepts about the deep circulation. These are that bottom water is formed in the Weddell Sea (Antarctic Bottom Water) and circulates around Antarctica, spreading northward into the three major oceans. Deep and bottom waters are also formed in the Norwegian and Greenland Seas, filling these basins and overflowing the Greenland–Faroes Ridge. As the water overflows, it mixes with other intermediate and deep waters. This overflow mixture makes up the bottom water to approximately 42°N in the western Atlantic. The overflow is also the source of part of the North Atlantic Deep Water which in the central and southern portions of the western Atlantic overlies the Antarctic Bottom Water. The bottom waters of the Indian and Pacific oceans are formed from mixtures of Antarctic Bottom Water, North Atlantic Deep Water, and some of the overlying waters. As the bottom water moves along its path it mixes with the overlying water, and this mixing increases its potential temperature in all oceans. Where it underlies more saline water (in the Atlantic, Indian, and southern South Pacific), it is made more saline. In the North Pacific, where the overlying water is low in salinity, the salinity of the bottom water decreases to the north.

In most areas the potential density of the bottom water decreases northward from the Antarctic region, through mixing with overlying waters that are lower in potential density, but along the western Atlantic the potential density is seen to increase toward the north. The temperature and salinity distributions of the bottom water in the western Atlantic indicate that the water has its source near Antarctica and spreads northward. Ordinarily one might suppose that the potential density of the water would decrease in deep water away from the source. Instead, the increase in potential density must arise from mixing Antarctic bottom waters with water of even higher potential density.

CHARACTERISTICS IN THE WESTERN ATLANTIC

Vertical sections of the distribution of potential density (σ_θ), potential temperature (θ) and salinity in the western Atlantic are shown in Figs. 4–6; the station positions are listed in Table 2 and shown in Fig. 7. The potential density has a maximum above the bottom between latitudes 40°N and 32°S shown by the 27·90- and 27·92-g/l. isopycnals. North of 40°N the maximum slopes upward from the bottom. Near

Table 2. Stations used in Atlantic Ocean vertical section.

Ship	*Station*	*Lat.*	*Long.*	*Date*	*Data source*
Anton Dohrn	1595	67° 33′N	24° 14′W	2 IV 57	Cons. Perm. Internat. Explor. Mer (1964)
	2268	65° 50′N	27° 50′W	17 III 58	Cons Perm. Internat. Explor. Mer (1965c)
	2283*	65° 16′N	31° 50′W	20 III 58	
	2313	63° 19′N	33° 40′W	5 IV 58	
	2317	61° 00′N	35° 40′W	6 IV 58	
Atlantis	5209	32° 01′N	52° 27′W	16 XI 54	Fuglister (1960)
	5462*	11° 27′N	50° 34′W	29 XI 56	
	5812	32° 26′S	38° 53′W	30 IV 59	
Chain	44	36° 17′N	53° 34′W	26 IV 59	Fuglister (1960)
Crawford	116	8° 18′S	31° 22′W	20 III 57	Fuglister (1960)
	127	15° 45′S	30° 59′W	4 IV 57	
	174	8° 14′N	45° 54′W	17 V 57	
	235	40° 15′N	41° 56′W	4 X 57	
	305	16° 14′N	56° 08′W	27 XI 57	
	423	24° 16′S	34° 00′W	10 X 58	
	495	0° 15′S	35° 01′W	27 XI 58	
Deutschland	125	75° 22′S	31° 55′W	29 I 12	Brennecke (1921)
	138	73° 34′S	33° 35′W	13 III 12	
Discovery	72	41° 43′S	42° 21′W	12 VI 26	Disc. Comm. (1929)
	1994	60° 36′S	26° 40′W	12 III 37	Disc. Comm. (1947)
	1996	62° 32′S	24° 32′W	13 III 37	
	1998	64° 16′S	22° 47′W	14 III 37	
	2000	66° 00′S	20° 54′W	15 III 37	
	2002	68° 19′S	17° 55′W	16 III 37	
	2004	69° 50′S	15° 29′W	17 III 37	
	3520	45° 17′N	43° 37′W	18 IV 57	Fuglister (1960)
	3615	24° 31′N	61° 08′W	20 X 57	
Eltanin	131	55° 54′S	24° 56′W	30 IV 63	Jacobs (1965)
	145	58° 34′S	23° 49′W	21 V 63	
	170	46° 50′S	35° 05′W	19 VIII 63	
	176	50° 21′S	35° 06′W	21 VIII 63	
Erika Dan	316	57° 26′N	43° 56′W	29 III 62	Woods Hole Oceanogr. Inst. MS data, NODC 31170
	320	54° 26′N	44° 59′W	30 III 62	
	339	49° 27′N	45° 10′W	9 IV 62	
G. O. Sars	179	74° 30′N	0° 37′W	23 IV 58	Cons Perm. Internat. Explor. Mer (1965b)
	185	76° 18′N	2° 00′W	25 IV 58	
	198	78° 16′N	0° 30′W	28 IV 58	
	318	72° 00′N	0° 45′W	14 VI 57	Cons. Perm. Internat. Explor. Mer (1963)
Pioneer	83	47° 11′N	160° 44′W	6 IX 62	U.S. Coast & Geod. Surv. MS data NODC 31099
Stranger (Leapfrog)	9	50° 57′N	172° 15′W	6 VIII 61	Scripps Inst. Oceanogr. (1965)
Johan Hjort	248*	70° 45′N	4° 15′W	29 V 58	Cons. Perm Internat. Explor. Mer (1965a)

*Only bottom values were used.

the equator it is at 3850 m; near 32°S it is at 3400 m. The potential density at the bottom is less than that at the maximum by about 0·03 g/l. (The narrow band of σ_θ greater than 27·88 extending from 2000 m at 57°S to 5000 m at 41°S is very marginally defined: with the available data it can neither be accepted as real nor entirely rejected and it will not be discussed further).

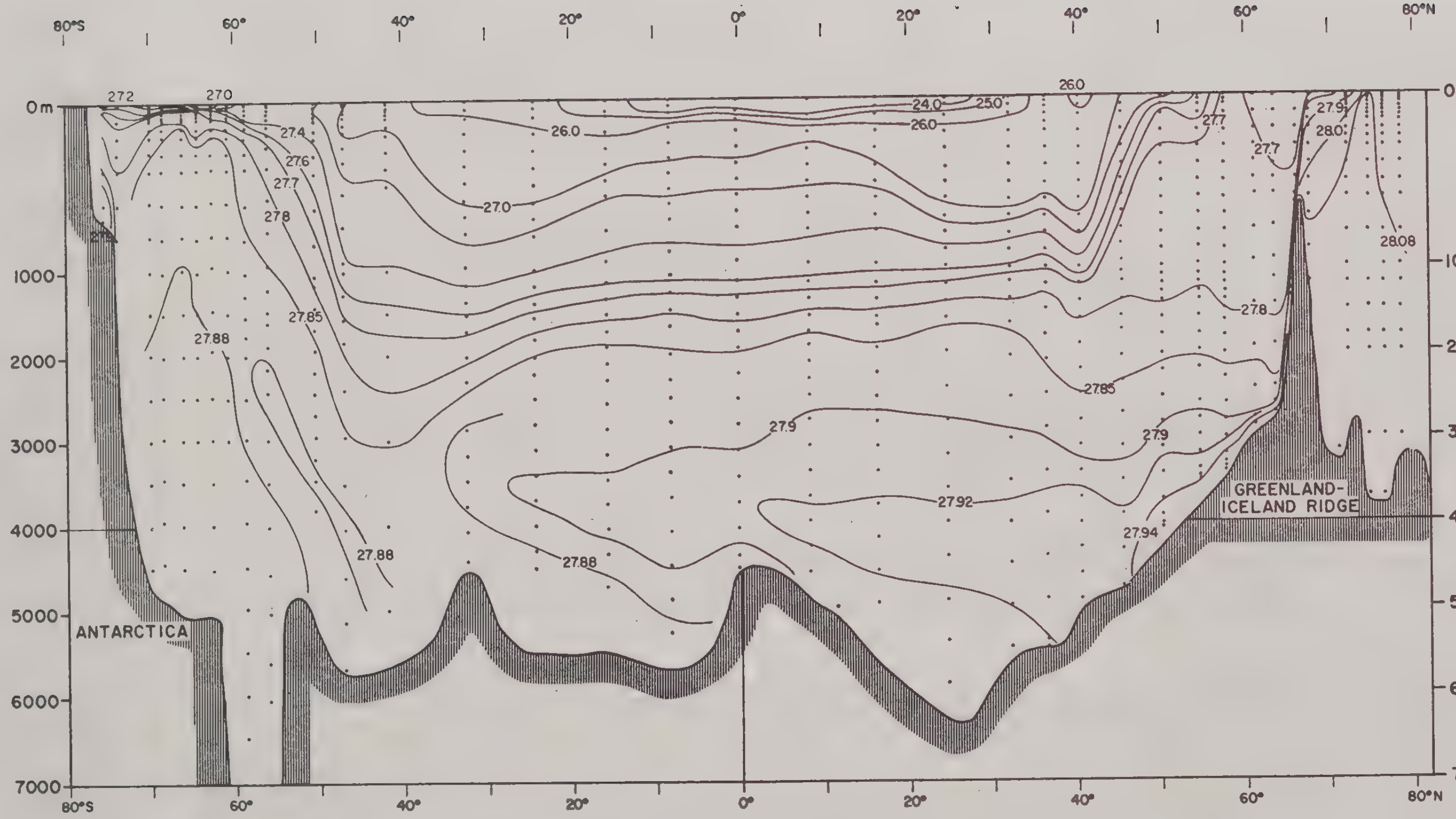


Fig. 4. Vertical section of potential density (σ_θ in g/l.) in the western Atlantic. Depth scale changes at 1000 m depth. Stations are identified in Table 2 and their positions are shown in Fig. 7.

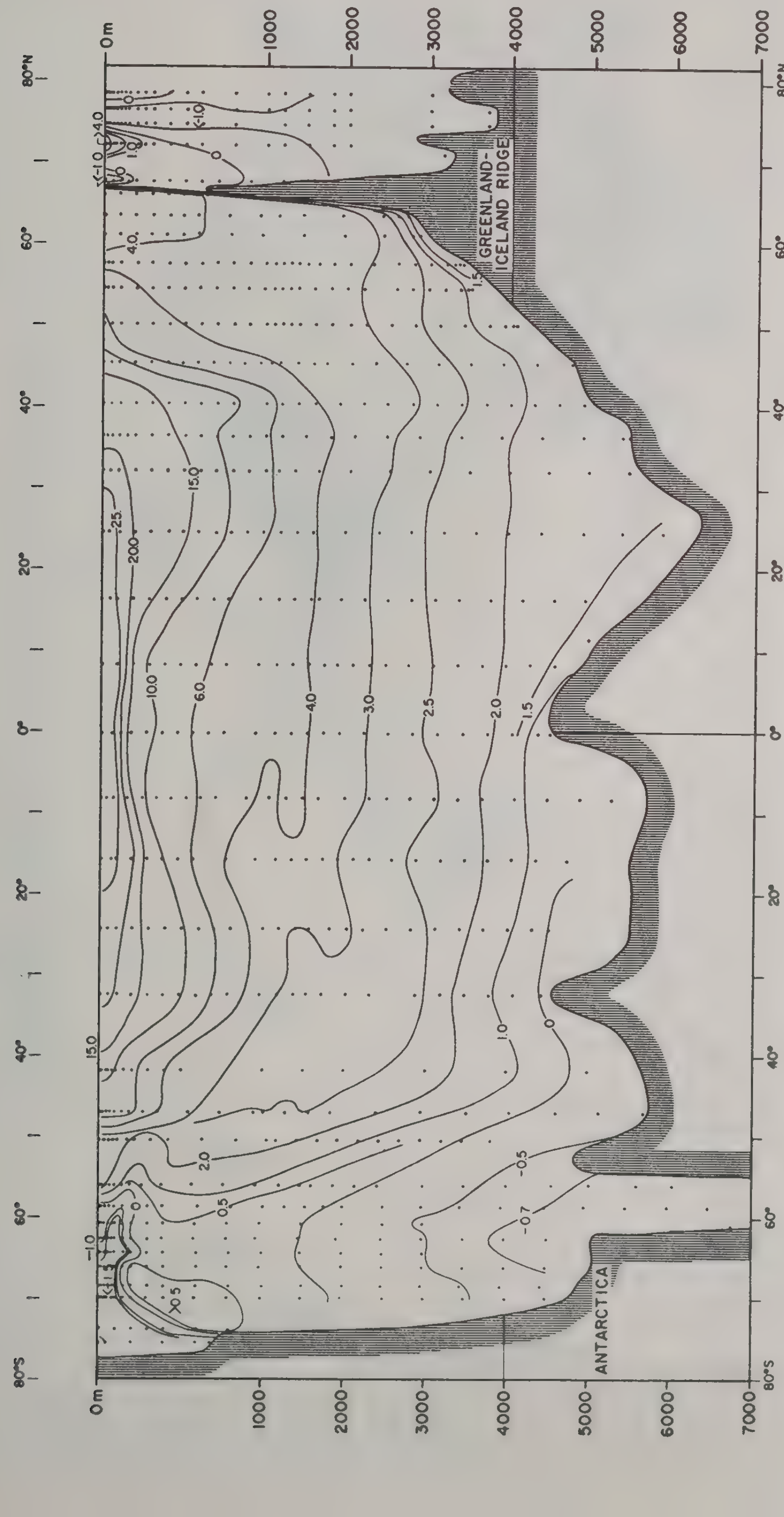


Fig. 5. Vertical section of potential temperature (θ. in °C) in the western Atlantic.

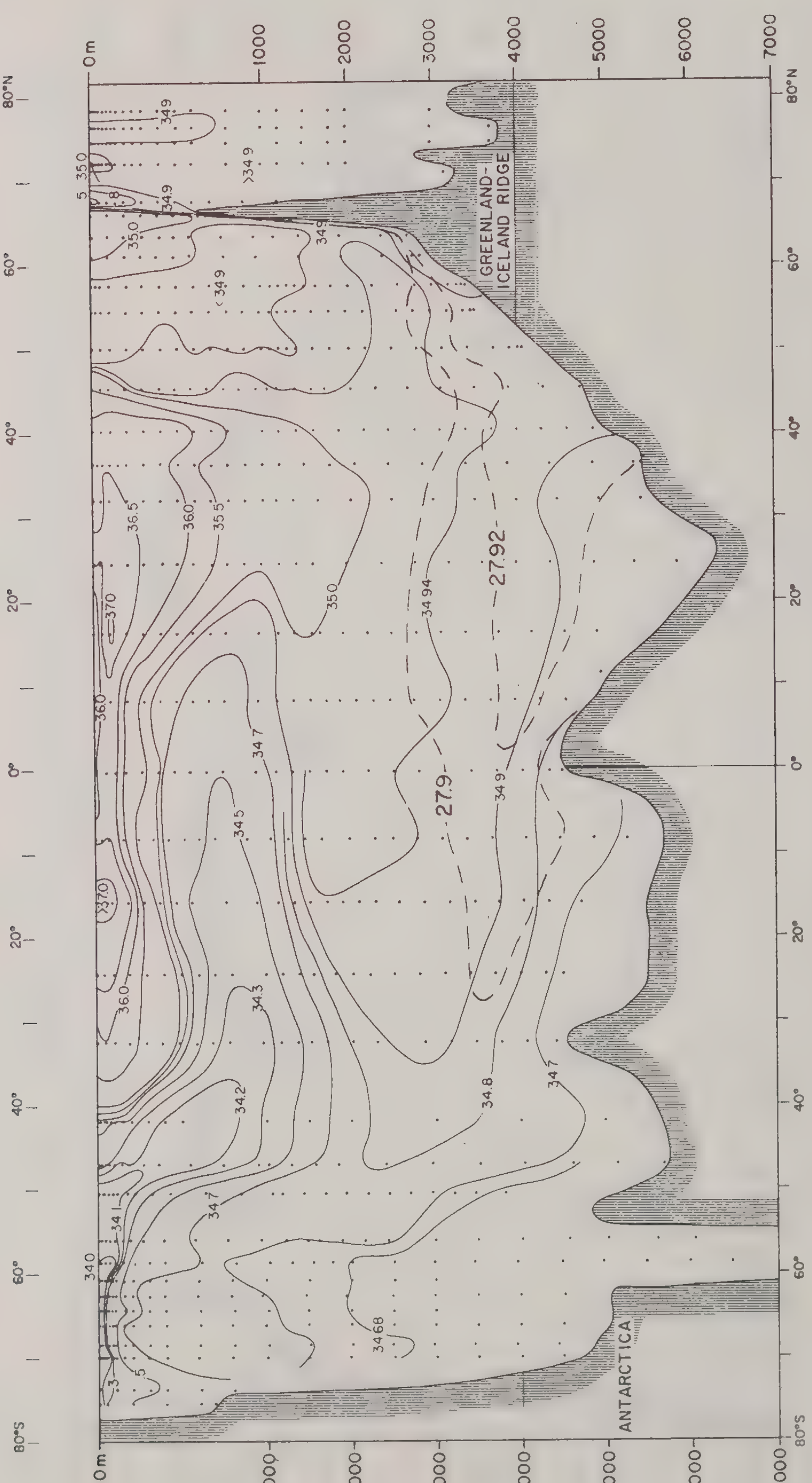


Fig. 6. Vertical section of salinity (‰) in the western Atlantic. Dashed lines indicate two isopleths of σ_θ (27·90 and 27·92 g/l.) taken from the field shown in Fig. 4.

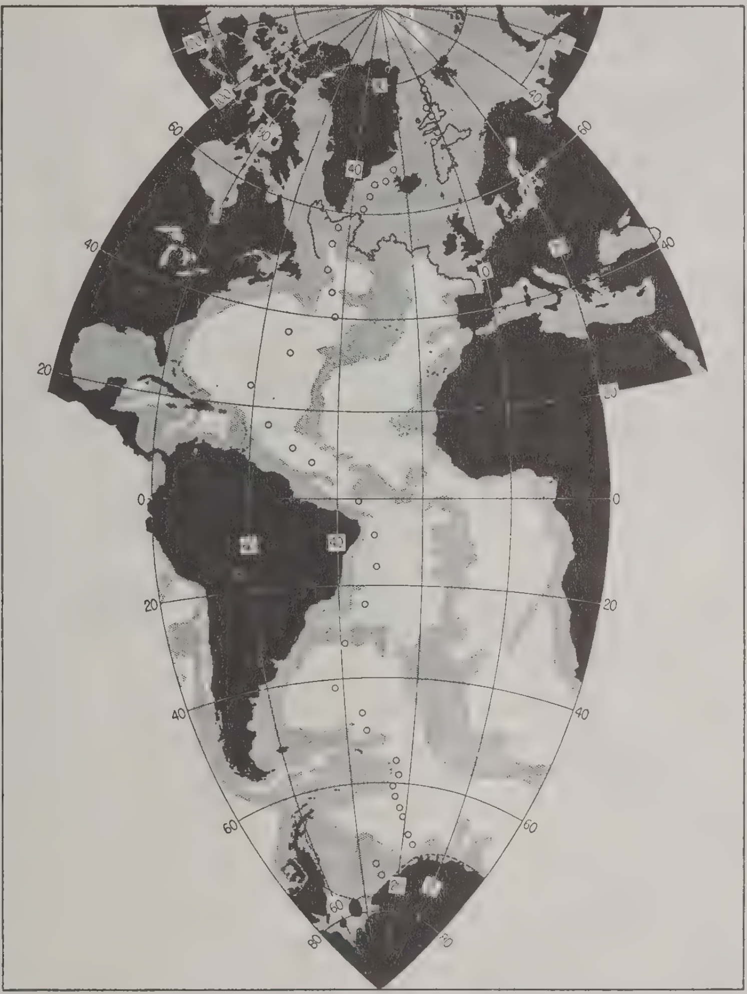


Fig. 7. Positions of the stations used on the vertical sections (Figs. 4–6, 10, 11). Stations are listed in Table 2. Depths less than 4 km are shaded. The 3-km isobath is drawn only in the northern Atlantic.

The water is, of course, stable; the inversion in potential density can occur under these stable conditions because the cold bottom water (Fig. 5) is more compressible than the warmer water at the potential density maximum. HESSELBERG (1918) defined stability as

$$\underset{\lim \partial z \to 0}{E} = \frac{1}{\rho}\frac{\delta\rho}{\partial z}$$

where $\delta\rho/\partial z$ is the individual density gradient defined by vertical displacement of a water parcel (as opposed to the geometric density gradient). For discrete samples the density difference ($\delta\rho$) between two samples is taken after one is adiabatically displaced to the depth of the other.

One can calculate the density a water sample would have if moved adiabatically to any depth, and compare it with the density any other sample would have. The density difference between two such samples moved to the same depth is a function of the depth (pressure) and is shown in Fig. 8 for two samples from *Crawford* Sta. 116.

One sample is from the depth of the potential density maximum and the other from near the bottom. The density difference varies with depth and changes sign near 850 m. Near the *in situ* depths of the samples the deeper sample is denser by approximately 0·15 g/l.; this is the $\delta\rho$ used in the stability formula. If both are raised to the sea surface (where their density would be potential density) the sample from near the bottom is less dense than the other by about 0·04 g/l. In this example the potential temperature of the deeper sample is lower by about 1·8°C and the salinity is lower by 0·2‰

The magnitude of the potential density inversion is approximately 0·03 g/l. in the area between the equator and 25°S. The maximum is equally consistent in magnitude and depth in zonal sections (west of the Mid-Atlantic Ridge). The measurements of temperature and salinity are apparently good enough to show that this small vertical difference in potential density is a real feature over a large area of the western Atlantic Ocean.

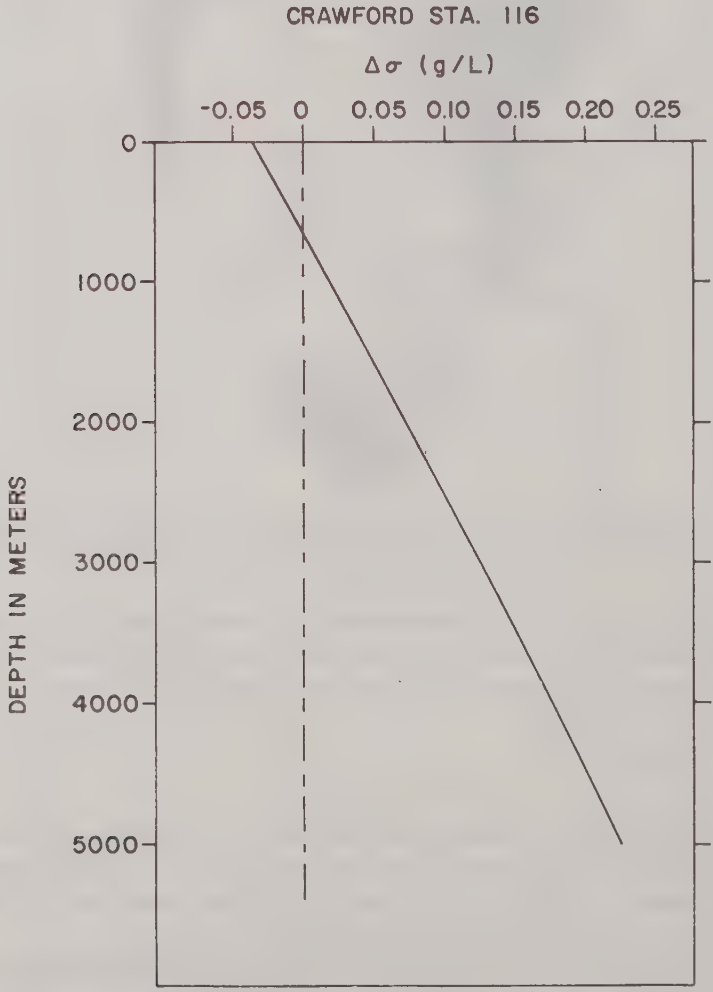


Fig. 8. Density difference between two samples from *Crawford* Sta. 116 moved abiabatically through the entire pressure (depth) range. The first (at 4085 m) is from the depth of the potential density maximum and the second (at 5285 m) is from near the bottom. Difference is taken from the first to the second.

Although the equation of state is imperfectly known for water at low temperatures and great pressures, the data shown in the figure do not suggest any internal inconsistencies in the present version.

Previous investigators have noted the inversion in potential density. WÜST (1933), in his discussion of the deep Atlantic, presented two meridional sections of potential density. His section for the west Atlantic is similar to ours in Fig. 4. He implied that for the water to be stable (which he believed it must be) the potential density must in fact increase monotonically from the sea surface to the bottom and concluded that the methods of determining density were not accurate enough. SCHUBERT's (1935) study of the stability of the Atlantic Ocean waters showed, however, that the deep water was stable. More recently WORTHINGTON and METCALF (1961) presented a mean potential temperature–salinity curve for the western Atlantic from which the potential density maximum can be inferred. Also Professor Raymond Montgomery has noted this inversion in his lectures. Lately KAWAI (1966) has also noted the potential density maximum above the bottom in the western Atlantic and has pointed out that the water is, however, stable: referring the deep-water temperatures and salinities to a common higher pressure, instead of one atmosphere, causes the calculated density index to increase monotonically with depth.

If subsurface waters attained their characteristics at or very near the sea surface, then potential density is useful for specifying the origin of these waters: because of the variation in compressibility, however, it does not directly specify the depths to which such waters might sink. Therefore the waters of highest potential density that flow over the Greenland–Faroes Ridge do not necessarily lie at the greatest depths when they flow southward in the western Atlantic. Instead they are confined to a layer above the Antarctic Bottom Water, which is lower in potential density but higher in *in situ* density at these pressures. A peculiarity of this distribution is that the northward-moving Antarctic Bottom Water, in mixing with the water above it, shows an increase in potential density along its path.

In Fig. 6, two isopleths of σ_θ are superimposed upon the salinity field. The σ_θ maximum is considerably deeper than the salinity maximum. The salinity maximum characterizes the upper and middle North Atlantic Deep Water (WÜST, 1935). The southward extension of the σ_θ maximum as shown by the 27·90 g/l. value approximately circumscribes the lower North Atlantic Deep Water and allows it to be clearly traced into the South Atlantic. It identifies this water as distinct from both the underlying cold, low-salinity Antarctic Bottom Water and the overlying warm, relatively more saline parts of the North Atlantic Deep Water. WÜST (1933), though he regarded the inversion in σ_θ as an artifact of various errors in the constants used in calculations, noted that potential density helped to distinguish Antarctic Bottom Water from water of North Atlantic origin. The characteristics at the maximum are very nearly the 2°C and 34·9‰ that WÜST (1935) estimated for lower North Atlantic Deep Water. MONTGOMERY (1958) estimated the volume of Atlantic Ocean water in classes defined by a potential temperature range of 0·05°C and a salinity range of 0·1‰. The primary mode, at 2·25°C, 34·95‰, represents North Atlantic Deep Water. Thus the core of water having a potential density greater than 27·9 g/l. south of the Greenland–Faroes ridges must occupy a large volume, as the figure suggests.

Although the isolines of σ_θ aid in locating the origin of this water and its southward spread to 35°S, they cannot tell us much about this water as it moves further south, beyond the clearly defined area of the σ_θ maximum.

South of 45°S the Lower North Atlantic Deep Water enters the strong eastward flow of the Antarctic Circumpolar Current. A preliminary examination of available data from regions to the east of this section has shown that the maximum might be traced farther southward. However, in the data available for this region, the salinity has been determined by titration. The limited precision of this method makes the definition difficult. In the deep water of this region and, near Antarctica, to within 500 m of the surface, σ_θ varies very little with depth, though the water is stratified and stable. If we wish to follow the lower North Atlantic Deep Water farther south we must choose some other characteristic.

DENSITY REFERRED TO 4000 DECIBARS

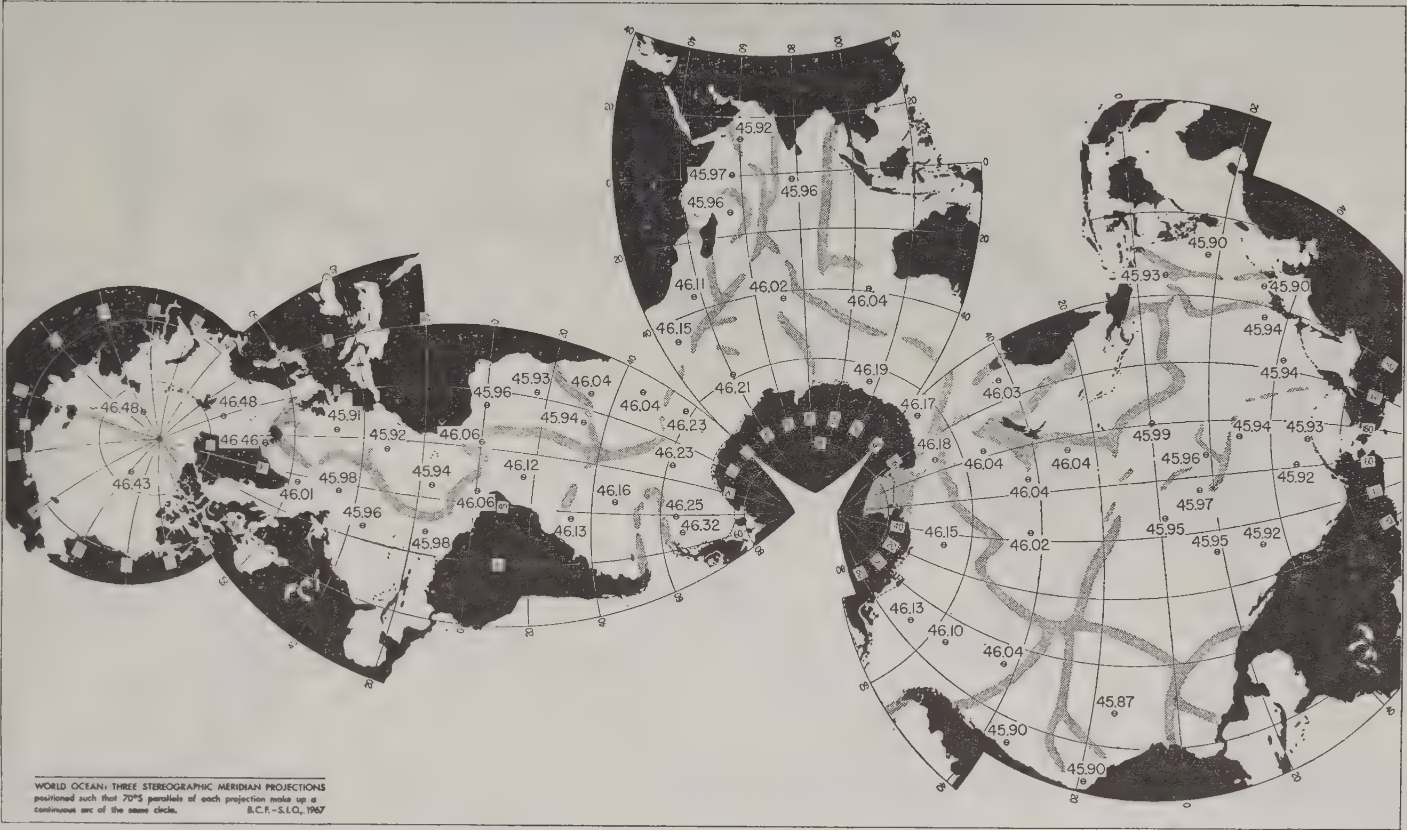
Abyssal waters

Limiting oneself to an examination of only the bottom values of potential density which increase to the north could have led to a faulty interpretation of the sense of flow. It is desirable to re-examine the density of the bottom water with a more appropriate density measure. Since the water is at great depth, we use the density the water would have if moved adiabatically, not to the sea surface, but to some common great depth. In this case we choose the depth where pressure is 4000 dbar. The symbol used will be ρ_4 (g/ml) or σ_4 (g/l.) in the ordinary σ-notation. *In situ* density at a depth where pressure is 4000 dbar is approximately 1·046 g/ml; or, in sigma units, 46 g/l. Thus the effect of this pressure is to increase the density by approximately 18 g/l. The amount of the increase in density varies slightly with the temperature and salinity (primarily the temperature) of the water; it is this variation that alters the relative distribution of σ_4 (Fig. 9) from that of σ_θ (Fig. 3). The coldest water shows the greatest density increase when the reference pressure is changed to 4000 dbar.

The highest value of σ_4 (46·48 g/l.) is found in the Norwegian basin, but this dense water is cut off from the major ocean basins to the south by shallow sills (approximately 600–900 m). South of the basin the highest value is found in the Weddell Sea (46·32 g/l.), and values decrease from there around Antarctica and into all other basins, with two exceptions. One of these is the small area near the Ross Sea noted before. The other is from Iceland to 40°N in the western Atlantic.

Potential temperature (Fig. 1) has a maximum near 45°N in the western Atlantic, indicating that the bottom waters from the Weddell Sea meet those from the north at about that latitude. Potential density, however, has a minimum near 47°S. When the density of the bottom waters is recalculated considering them moved adiabatically to a pressure of 4000 dbar, the density (σ_4) minimum appears, as with the potential temperature, near 45°N. Thus, the distributions of density referred to a pressure near the *in situ* pressure substantiates the conclusions drawn from the picture of potential temperature.

Since the colder waters are more compressible, the gradients of σ_4 (Fig. 9) are greater than those of σ_θ (Fig. 3). The north–south gradients in the Indian and Pacific oceans are approximately three times greater for σ_4 than for σ_θ. While σ_θ remains almost constant around Antarctica, σ_4 decreases monotonically from the Weddell Sea to the Pacific–Antarctic basin (except for the station near the Ross Sea). The lowest values of σ_4 are found in the eastern Pacific, which has relatively warm, low-salinity


WORLD OCEAN: THREE STEREOGRAPHIC MERIDIAN PROJECTIONS positioned such that 70°S parallels of each projection make up a continuous arc of the same circle. B.C.F.–S.I.O., 1967
46.48
46.48
46.46
46.43
45.91
45.92
45.98
46.01
45.96
45.96
45.93
46.04
45.94
46.06
45.94
46.12
46.06
45.98
46.13
46.04
46.23
46.23
46.16
46.25
46.32
45.92
45.97
45.96
45.96
46.11
46.02
46.04
46.15
46.21
46.19
46.17
46.18
46.03
46.04
46.04
46.04
46.15
46.02
46.13
46.10
46.04
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45.90
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45.97
45.95
45.95
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Fig. 9. Density (σ_4) the abyssal waters would have if moved adiabatically to the depth where pressure is 4000 dbar. Units are g/l.

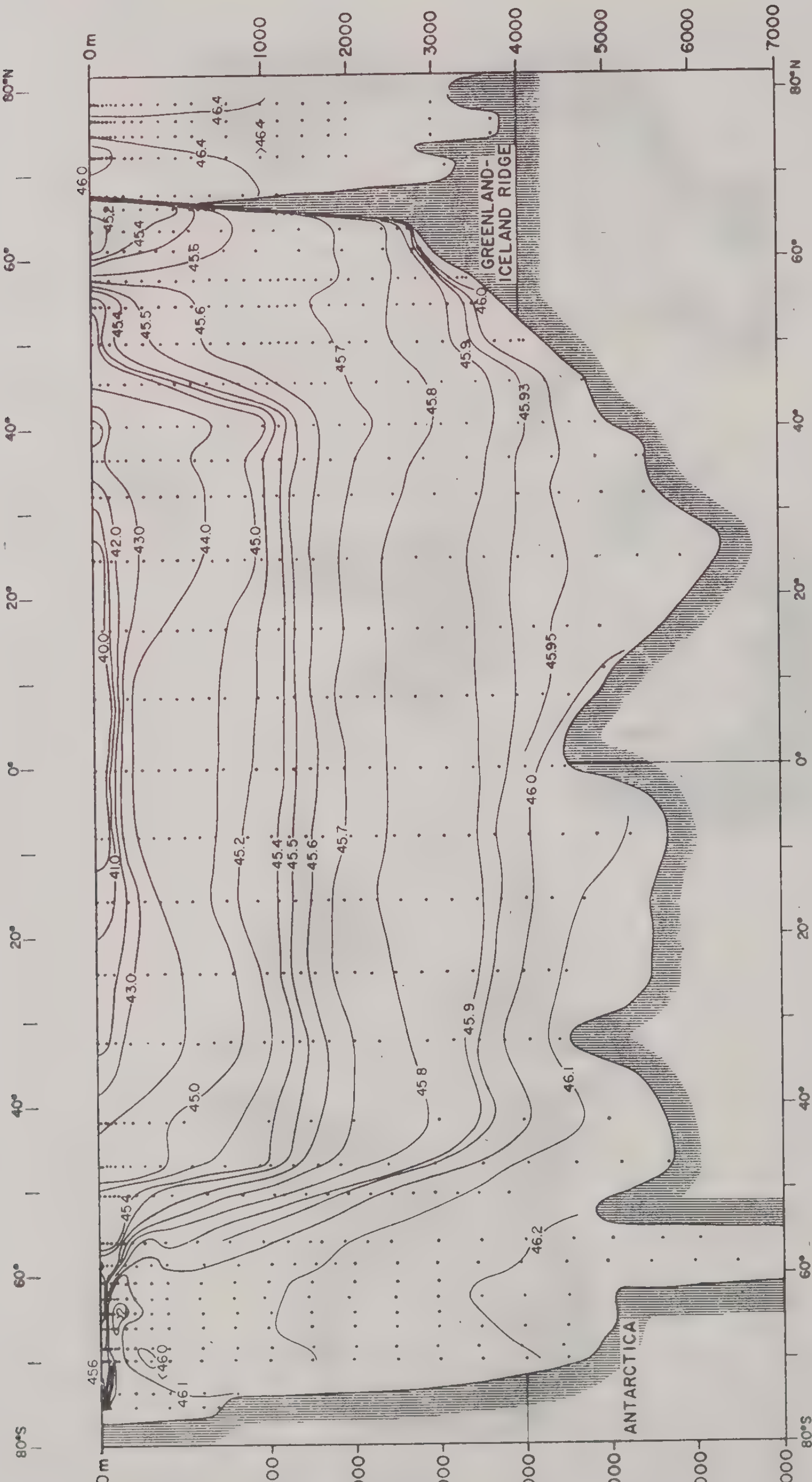

Fig. 10. Vertical section in the western Atlantic showing the density (σ_4 in g/l.) the water would have if moved adiabatically to the depth where pressure is 4000 dbar.

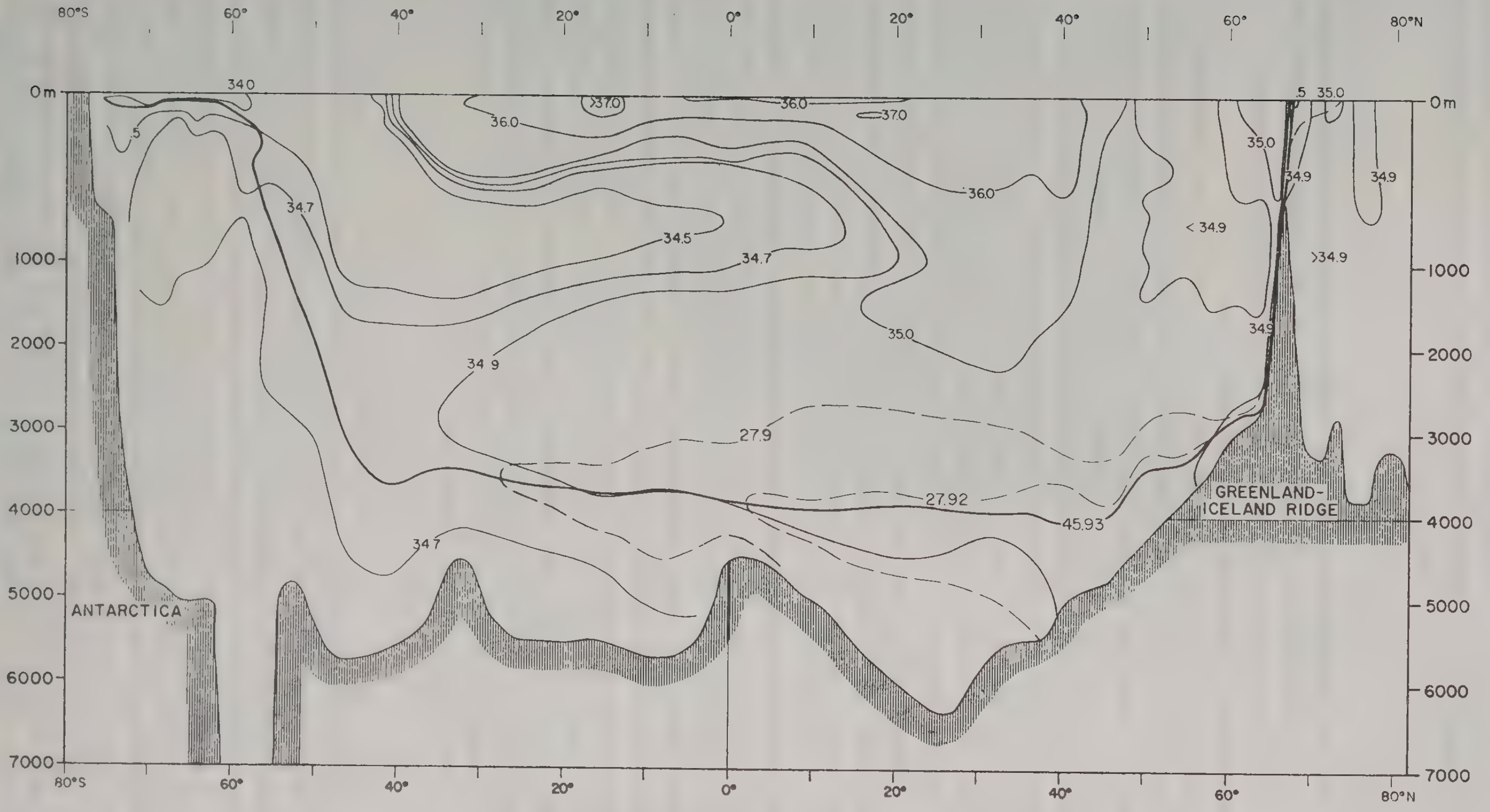

Fig. 11. Vertical section in the western Atlantic of salinity (‰) with the isopleths of $\sigma_\theta = 27{\cdot}90$ and 27·92 g/l. (light dashed line) and of $\sigma_4 = 45{\cdot}93$ g/l. (heavy line) taken from the fields of Figs. 4 and 10 respectively.

water, and the eastern North Atlantic, which holds the warmest and therefore the least compressible of the abyssal waters.

Western Atlantic

We now return to examine the western Atlantic: it is here where we find the major sources of deep and abyssal waters. The density field can be recalculated referred to a deep pressure surface, as we did with the bottom observations. Because the σ_θ maximum is found near 4 km we again choose 4000 dbar.

The field of σ_4 (Fig. 10) is smooth and, from intermediate depths, monotonically increases to the bottom. Near the surface in the far south σ_4 shows an inversion just as σ_θ does at great depths: such peculiarities may occur whenever density is calculated from a pressure very different from the *in situ* pressure. Thus the fields of potential density or density referred to various pressures adequately represent the density stratification only within some appropriate depth range.

In the method of isentropic analysis isopycnals of σ_θ are assumed to represent mixing surfaces. This method of analysis has been restricted to depths which rarely exceed 1000 meters. Except for a different choice of reference pressure, this new density, σ_4, is defined in the same way as σ_θ. The same assumptions about mixing surfaces hold for σ_4 at great depths as for σ_θ near the sea surface. The field of σ_4, therefore, may serve as a useful representation of flow and mixing at great depths.

The value of σ_4 which most closely coincides with the σ_θ maximum is 45·93 g/l. In Fig. 11 this isopleth is shown superimposed on the fields of σ_θ and salinity. Beyond the area of the clearly defined σ_θ maximum we can define the water by this isopleth. The isopleth rises abruptly towards the south at about 50°S, in the Antarctic Circumpolar Current, as does the salinity maximum. In fact it rises so far that it leaves its reference pressure far behind, and probably losses its validity as a tracer of flow or mixing. Instead, where the isopycnal rises, one might try to change the reference pressures to correspond to the depth changes and construct a mixing-line of short segments of such density-lines, each referred to the appropriate pressure. In this way one might be able to trace the water masses from ocean to ocean through the Antarctic Circumpolar flow, where depth variations are so great that any single reference pressure can be severely misleading.

CONCLUSION

We have examined the abyssal properties in the world ocean with the newer data and found them consonant with the conventional notions of deep flow except for potential density, which at first appears not to fit in the Atlantic. Further examination of this has revealed that there is a potential-density maximum above the bottom in the western Atlantic, and that this represents fairly well the lower North Atlantic Deep Water. Examining the deep waters by referring density to a more appropriate pressure eliminates the inversion and clarifies the density changes along the bottom. Also these isopycnals may extend the usefulness of isentropic analysis to great depths. One of these density surfaces has been shown to coincide with the σ_θ maximum and allows one to trace this water considerably farther south, past the region where the maximum is well defined. It may be possible to trace water masses even farther, through the Antarctic Circumpolar Current where wide depth variations complicate the problem, by choosing appropriate reference pressures as the depth of a water mass varies and by constructing mixing-paths made of short segments of such density-lines, each referred to the appropriate pressure.

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FECUNDITY OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* GIRARD[1]

JOHN S. MacGREGOR
U.S. Bureau of Commercial Fisheries
Fishery-Oceanography Center
La Jolla, California 92037

The ovaries and ovarian eggs of the northern anchovy are described briefly and compared with those of two other engraulids, *Cetengraulis mysticetus* and *Anchoa naso*. The number of eggs spawned in one batch by *E. mordax* was estimated to be 574 per g of total weight of the female compared with 836 for *C. mysticetus* and 326 for *A. naso*. Other factors used to determine biomass of adult anchovies from planktonic egg census data are discussed. The biomass of adult male anchovies in the commercial catch was about 75% of that of adult females. Therefore, for one spawning, 5.2×10^8 eggs would be produced per short ton of female anchovy or 3.0×10^8 eggs per short ton of adult biomass. The average number of times each female anchovy spawns in a year is not known and may vary from year to year.

INTRODUCTION

One of the objectives of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) is to obtain censuses of the pelagic eggs and larvae of important fish species in the CalCOFI survey area. These data have been used directly as indices of relative sizes of the adult populations that produced them. Additional information, such as may be derived from fecundity studies, helps to refine these estimates of adult population size.

Northern anchovy larvae are the most abundant of any species taken in the survey area. More than a third of all larvae taken over the past 15 years have been anchovies, and they have increased in recent years both in total numbers and in percentage of all larvae taken. Plankton nets used in the CalCOFI surveys, which were designed to retain the larger, spherical planktonic fish eggs, do not retain all of the smaller, oblong anchovy eggs. Although supplementary hauls with finer mesh nets that retain all anchovy eggs have been used in recent years, presently available data on comparative abundance of the various fish species are based on larval abundance.

Although the literature contains considerable information on the northern anchovy, nothing has been published on its fecundity. The purpose of this paper is to present the fecundity data now available, and to discuss their application to the problems of estimating adult populations.

MATERIALS AND METHODS

The data on anchovy fecundity were obtained from 19 females collected off California or Baja California. Two were taken near the entrance to San Diego Bay, March 29, 1951; 11 were from bait samples collected near San Diego, March 29, 1960; 3 were collected at CalCOFI station 90.30, in the southern Santa Catalina Channel, July 20, 1953; and 3 at station 113.35, 55 nautical miles due north of San Benitos Islands, Baja California, September 21, 1952. The fish were preserved in formalin at the time of collection. The data, recorded after preservation, include standard length, weight, ovary weight, and number and size of eggs (Table 1). The methods used were similar to those of MacGregor (1957). Comparative data for the anchoveta, *Cetengraulis mysticetus,* are from Peterson (1961) and for *Anchoa naso* from seven females collected off Baja California.

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[1] Accepted for publication April 1968.

TABLE 1

Measurements and Counts Related to Fecundity of *Engraulis mordax* and *Anchoa naso.*

Standard length (mm)	Weight (g)	Gonad weight (g)	Advanced eggs		
			Number		Size range (mm)
			Total	Per g of fish	
Engraulis mordax					
97	9.6	0.322	4,025	419	0.62–.78
102	10.7	.766	8,647	808	.66–.84
106	12.3	.389	6,956	566	.52–.66
108	11.8	.501	5,487	465	.66–.76
108	13.9	.859	10,160	731	.68–.80
109	13.9	.602	7,150	514	.58–.70
109	12.7	.730	8,546	673	.68–.86
111	14.4	.536	8,049	559	.54–.62
111	15.0	1.136	11,061	737	.68–.82
113	15.1	.951	8,346	553	.68–.80
114	14.4	.862	6,619	460	.64–.78
120	21.5	.692	7,895	367	.56–.78
121	18.6	.654	10,700	575	.52–.66
124	21.0	1.288	15,519	739	.64–.82
128	26.5	1.288	12,836	484	.70–.80
130	24.5	1.842	18,579	758	.72–.86
130	27.5	.832	12,962	471	.50–.66
131	26.0	.642	10,289	396	.50–.58
138	33.9	1.763	21,297	628	.62–.78
Anchoa naso					
50	1.36	.021	346	254	.30–.42
52	1.57	.023	340	217	.34–.46
58	2.01	.030	375	187	.32–.40
76	5.15	.090	926	180	.30–.40
75	4.00	.120	970	209	.34–.42
78	5.29	.215	2,888	546	.34–.44
81	6.17	.309	4,231	686	.34–.44

DESCRIPTION OF GONADS AND OVARIAN EGGS

The gonads of *E. mordax* and *A. naso* are elongate, tapered posteriorly, and not fused. Both the shape and lack of fusion seem to be typical of clupeoids. Since the gonads are the last organs to develop, and because no special space is provided for them, they tend to crowd into whatever space is available. They assume the general shape of the body cavity and are contoured on one side by the body wall and on the other side by the other internal organs.

The gonads of *C. mysticetus* differ from those of the other two species in being tapered anteriorly (this species has a deeper body and a larger body cavity posteriorly) and joined posteriorly.

The gonads of *A. naso* and *E. mordax* resemble those of most fish species in that the left gonad is usually larger than the right. In *E. mordax,* the left gonad composed 49 to 62% of the total gonad weight for 29 females and 46 to 62% for 13 males; in *A. naso,* the percentages were 48 to 65 for 7 females and 50 to 60 for 6 males. The average for each of the four groups was between 55 and 56%. No data are available on the comparative size of gonads of *C. mysticetus.*

While most fish eggs are spherical, engraulid eggs are more or less oval. The length of the planktonic eggs of 10 species of engraulids from the Gulf of Panama (Simpson, 1959) ranged from about 1½ to 2¾ times their width. Bolin (1936) described the planktonic egg of *E. mordax* as ellipsoidal, 1.23 to 1.55 mm long by 0.65 to 0.82 mm wide, with a segmented yolk, no oil globules, and no sculpturing on the membranes. The latter three characteristics were present in all engraulid eggs sampled by Simpson.

The formalin-preserved ovarian eggs of *E. mordax* are transparent and spherical up to a diameter of 0.14 mm, but larger eggs are elongate. The eggs are translucent and darker at 0.20 mm because of yolk formation, and become opaque as size and yolk content increase. The largest ovarian eggs I found were 0.86 mm long.

The eggs of *A. naso* are spherical throughout their ovarian development. Yolk begins to form in eggs of 0.10-mm diameter. The largest ovarian eggs measured 0.46 mm. Among the 14 species of engraulids examined by Peterson (1956), *A. naso* was one of three that had spherical ovarian eggs; the others had oval eggs. The egg developing within the ovary has no perivitelline space and has the same shape as the yolk. After spawning, the yolk, enclosed in the vitelline membrane, apparently retains the same shape—either spherical or more or less ovate—that it had within the ovary, but the shell of the egg becomes ovate. Among the engraulid eggs in plankton figured by Simpson (1959), some oval eggs had oval yolks and others had round yolks.

The ovarian eggs of the anchoveta are oval. Peterson (1961) reported ovarian eggs of this species up to 0.66 mm long, while Simpson found that planktonic eggs average 1.17 mm long and 0.56 mm wide.

NUMBER OF EGGS PER SPAWNING

The number of eggs per spawning is assumed to equal the number of eggs in the most advanced modal group in the ovaries. As in other fishes, the number of advanced eggs tends to increase as fish size increases. Generally the number of eggs is proportional to the weight of the fish and to the cube of the standard length. However, in many species egg production occurs over such a relatively short range of fish lengths, and variation in the number of eggs produced at each length is so great, that the relationships of length and weight to egg production are masked. As a rule of thumb, the curvilinear relationship between standard length and number of eggs produced is not apparent unless the largest fish in the sample is more than twice as long as the smallest fish.

Peterson (1961) fitted a least squares straight line to his length-fecundity data for the anchoveta, $E = 101{,}200 + 1{,}0006L$, in which E = the number of ova in the spawning mode and L = standard length in mm. His largest fish (162 mm) was only 1.4 times the length of the smallest (115 mm), and he found no indication of a significant departure from a linear relationship.

In my sample of 19 anchovies, the length of the largest fish (138 mm) also was only 1.4 times the length of the smallest fish (97 mm); the straight-line relationship is $E = 2{,}175 + 7.700L$. The parabolic curve based on the cube of length is $E \doteq 0.00646L^3$, and that based on the log-log transformation is $E = 0.000574L^{3.5}$. The respective correlation coefficients are 0.816, 0.820, and 0.830, which, though highly significant, are not significantly different among themselves. If the range of lengths of the fishes could be increased, the curvilinear relationships should become progressively better than the straight-line relationship.

Although in the present samples the correlation coefficient from the log-log transformation is slightly better than that based on the cubic relation, the latter will often yield a lower variance and higher correlation coefficient. This relation also holds for the length-weight curve. The log-log line heavily weights lower numbers in its transformation, resulting in a parabolic curve that is only a rough and often misleading approximation of the best fitting curve. If spawning occurs over a restricted range of fish lengths, the straight-line relationship is practical, whereas if the length range is greater, the cubic relationship is generally satisfactory.

For some purposes, weight-fecundity relationships are more useful than length-fecundity. An understanding of weight-fecundity relationships may most easily be obtained by determining the number of advanced eggs produced per unit of fish weight. The mean numbers of advanced eggs per gram of fish were 574 for 19 *E. mordax,* 836 for 86 *C. mysticetus,* and 326 for 7 *A. naso.*

The number of eggs per g of fish does not appear to change with size of *E. mordax;* therefore, the weight-fecundity relationship may be described by $E = 574\ W$ in which E = the estimated number of advanced eggs in the ovary and W = fish weight in g.

Peterson (1961) fitted a least squares straight line to his anchoveta weight-fecundity data and obtained $E = 3{,}304 + 927\ W$. The large negative y-intercept indicates that the number of eggs is not proportional to fish weight but gradually increases with increasing fish size. A comparison of eggs per g of fish for the various sizes of anchovetas does not bear out this indication. The 13 smallest fish, 115 to 120 mm SL, have a mean of 533 eggs per g of fish (standard error of the mean = 35) and the remaining 73 fish, 121 to 162 mm SL, have a mean of 890 eggs per g of fish (standard error of the mean = 26). The number of eggs per g of fish does not change significantly among these remaining 73 fish; the mean is 927 eggs for the 13 smallest (121 to 128 mm) in this group and 874 for the 13 largest (153–162 mm). If the fecundities of these two groups are representative of the size groups in the population, it might be more practical to use the formulae $E = 533\ W$ for fish up to 120 mm SL and $E = 890\ W$ for larger fish.

The smaller specimens in a number of fish species have a lower fecundity, but the increase in fecundity with size tends to be abrupt rather than gradual. In *A. naso,* the five smaller specimens (50 to 76 mm) averaged 209 (180 to 254) eggs per g of fish, whereas the two larger specimens (78 and 81 mm) averaged almost three times as many, 616 (546 and 686).

Although only 19 anchovies were used to determine fecundity, the resulting data should be satisfactory for census purposes if the sample is representative of the population. Eggs per g of fish were almost identical for different areas (Santa Catalina, San Diego, San Benitos) and different seasons (March, July, September) as well as for different sizes of fish. Therefore, in spite of the small sample, I believe that it is representative of the northern anchovy population.

The mean number of eggs per g of fish, 574, has a standard error of 30. The 95% fiducial limits are ± 60 eggs per g or ± 10%. For the much larger sample of anchovetas, the 95% fiducial limits are ± 54 eggs or about ± 6%.

THE RELATION OF FECUNDITY TO THE ESTIMATION OF BIOMASS OF ADULT ANCHOVIES

To determine the biomass of the adult anchovy population from egg census data, we must know the sex ratio of the population by weight, the average number of times the population spawns during the egg census period (1 year for the present study), and the number of eggs per spawning.

Of 3,500 anchovies sampled during the 1952–53 and 1953–54 seasons (for which length and sex are available), 1,545 were males and 1,955 were females (Miller et al., 1955). The number of males equaled 79% of the number of females. The males averaged 138.5 mm SL and the females 142.2 mm SL. If we assume that there is no great difference in form between male and female anchovies then, mean SL^3 of females is to mean SL^3 of males as mean weight of females is to mean weight of males. From this we can determine that the mean weight of males was about 92% of the mean weight of females. Multiplying percentage weight by percentage numbers gives a male biomass equal to 73% of the female biomass.

Weight and sex data are available for a sample of 336 anchovies taken from the San Francisco area between September 1952 and February 1953. The 181 females averaged 149.5 mm SL and weighed a total of 6,652 g; the 155 males averaged 145.3 mm SL and weighed a total of 5,172 g, or about 78% of the total weight of the females.

From these data we may assume that the biomass of male anchovies available to the fishery equals about 75% of the female biomass. If for one spawning a female produced 574 eggs per g of body weight, 5.2×10^8 eggs would be produced per short ton of female biomass; therefore, we should expect the same number of eggs per 1.75 short tons of adult anchovies or about 3.0×10^8 eggs per ton of adult anchovies.

The number of times an anchovy spawns in one season is not known. There has been some speculation that the prespawning ratio of small yolked eggs to large yolked eggs in the ovary is an indication of the number of spawnings that will take place in that spawning season. That is, if the ratio is approximately one to one at the beginning of the spawning season, there will be two spawnings; if it is two to one, there will be three spawnings, etc. As the spawning season progresses, the ratios would decrease by one after each spawning. This speculation is not supported, however, by my data for anchovies (nor by much more extensive unpublished data for sardines). Ratios apparently are not related to size of fish, area, or season. Ratios for individual fish ranged from 1.3:1.0 to 2.4:1.0. The mean ratios for fish in the present collections were 2.2:1.0 (San Diego, March 1951), 1.9:1.0 (San Diego, March 1960), 1.7:1.0 (Santa Catalina Channel, July 1953), and 1.8:1.0, (San Benitos Islands, November 1952).

The anchovy with the 2.4:1.0 ratio was most nearly ripe, and had eggs up to 0.86 mm long. It was also the only fish that exhibited a distinct trimodal distribution of yolked egg sizes. The ratios of the numbers of eggs in each mode, from smallest eggs to largest, were 1.4:1.0:1.0. If the largest eggs were omitted, the remaining distribution would closely approximate the lower ratios in anchovies in which eggs in the most advanced group were smaller. In addition, a number of the female anchovies examined could not be used for fecundity estimates because they contained only small, yolked eggs with a unimodal size distribution. The eggs in a few of these fish appeared to be undergoing resorption.

The ovaries offer no evidence of a fixed number of spawnings. The egg ratios suggest that the anchovy may spawn one, two, three, or more times per year; the eggs remaining after a given spawning might either be resorbed or be replenished from the reserve of non-yolked eggs. If replenishment does occur, the ratios are even less meaningful.

In 19 anchovetas, the eggs in the advanced mode averaged more than three times as many as the smaller yolked eggs (Peterson, 1961). Howard and Landa (1958) noted the paucity of smaller eggs in this species and concluded that only one batch of eggs was spawned, following which the smaller eggs were resorbed. The short spawning season of the anchoveta also supports the idea of a single spawning. Almost all anchoveta eggs taken in plankton tows in the Gulf of Panama were collected in November and December, and neither eggs nor ripe fish could be found from mid-January to October (Simpson, 1959).

In *A. naso*, ratios of small yolked eggs to large yolked eggs ranged from 0.0:1.0 to 4.2:1.0. Fish with developing ovaries have been taken in Costa Rica in August, September, and January (Peterson, 1956), and my two samples from Baja California were taken in July and November. A protracted spawning season and multiple spawning are indicated.

The spawning season of the northern anchovy also is protracted; some spawning occurs in every month, and fish with developing ova may be found at any time of year. Nevertheless, there is a definite annual peak in spawning, as shown by the number of anchovy larvae taken in plankton tows off the California and Baja California coasts during the 7 years 1951 through 1957 (Ahlstrom, 1953, 1954, 1958, 1959; Ahlstrom and Kramer, 1955, 1956, 1957). Peak spawning occurred in March (4 years) February (2 years), and January (1 year), and spawning during the peak month included 20 to 33% of the total spawning for each year.

During the early part of the year, almost all of the mature females in the population contain well-developed eggs or are recently spent; consequently, later spawnings must represent repeat spawnings by at least part of the population, although younger, late-maturing females may contribute. If the average time required to mature a second batch of eggs after spawning of the first batch was one month, if all adult females spawned in the peak month, and if 20 to 33% of the year's spawning took place in the peak month, an average of three to five spawnings per year would be indicated. The percentage of annual spawning ranged from 34 to 49 for the 2 consecutive highest months over the 7-year period. If the spawning interval were 2 months, an average of two or three spawnings would be indicated.

The hake, *Merluccius productus*, which occurs in the same area and has a peak spawning period very similar to that of the anchovy, spawns only once a year (MacGregor, 1966). Larval occurrence indicates that 18% of the hake spawning takes place in January, 36% in February, 35% in March and 10% in April, with the remaining 1% scattered through the next 8 months. The percentage of hake spawning for the four peak months is about double that of the anchovy. If egg development and spawning are otherwise similar, but the hake spawns only once a year, we might postulate that the anchovy spawns an average of twice a year.

If one spawning produces 3×10^8 eggs per short ton of spawning fish, two spawnings would produce 6×10^8, three spawnings 9×10^8, and four spawnings 12×10^8 eggs per ton. If we arbitrarily estimate the average number of spawnings a year to be two and a half, and the actual number was only one, then the actual biomass would be 250% of our estimated biomass; if the actual number of spawnings was two, actual biomass would be 125% of that estimated; if three, 83%; and if four, 63%. Not knowing the average number of spawnings per year can introduce considerable error into the calculations.

The number of eggs spawned per unit of fish weight for one spawning and biomass ratio by sex probably change so little from year to year that data obtained in one year could be used for any other year. The number of spawnings, however, could change from year to year, depending on the size composition of the spawning stock or on hydrographic conditions. Another factor affecting calculations would be the change in biomass that results from the maturation of juvenile fish and mortality of adults during the year. Biomass estimates would be an annual mean value weighted to heaviest periods of spawning.

Probably a better way to estimate the adult population on the basis of egg counts would be to sample intensively during a period of peak spawning. If we could determine, by sampling, that portion of the adult population which had spawned once during one or two of the peak spawning months of a given year, we could calculate the average biomass existing at that time from an egg census covering the same period. This procedure largely would eliminate problems arising from weighted annual biomass estimates, multiple spawning, and changes in number of spawnings from year to year.

SUMMARY

The number of advanced eggs produced per unit of fish weight was 574 eggs per g of female for *E. mordax*, 836 for *C. mysticetus*, and 326 for *A. naso*. Although the number of eggs per gram of fish did not change with size of fish for *E. mordax*, it was considerably higher for larger specimens of each of the other two species.

The biomass of male anchovies in California commercial landings equaled about 75% of the biomass of females. Therefore, on the basis of one spawning, 3.0×10^8 eggs would be produced per short ton of spawning adult anchovies. The number of times a female anchovy spawns in a season cannot be determined from presently available data.

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AVOIDANCE REACTIONS OF A MOLLUSC *BUCCINUM UNDATUM* TO SAPONIN-LIKE SURFACE-ACTIVE SUBSTANCES IN EXTRACTS OF THE STARFISH *ASTERIAS RUBENS* AND *MARTHASTERIAS GLACIALIS*

A. M. MACKIE, R. LASKER* and P. T. GRANT

N.E.R.C. Fisheries Biochemical Research Unit, University of Aberdeen,
Scotland

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Abstract—1. Saponin-like substances present in extracts of *Asterias rubens* and *Marthasterias glacialis* were isolated and partially characterized.

2. Microgram quantities of these saponins and some other surface-active agents elicited either an immediate avoidance reaction or an involuntary series of convulsions in *Buccinum*. The type of response was dependent on concentration.

3. A sensitive, semi-quantitative assay was developed using the withdrawal response of the foot-muscle of intact *Buccinum*.

4. The response of the foot-muscle of intact *Buccinum* towards purified preparations was not accurately reflected by a bio-assay procedure involving an isolated radula muscle of *Buccinum*. The latter but not the former required the presence of a protein fraction as well as the saponin-like substance for a significant response.

5. The relative specificity of these saponin-like substances and other surface-active agents towards *Buccinum* has been studied. It is suggested that they stimulate or damage chemosensory cells on the surface of the foot-muscle.

INTRODUCTION

THE VARIED responses of molluscs and to a lesser extent anemones and echinoderms towards asteroids (starfish) have been well documented (Feder & Christensen, 1966). There is some evidence that the response shown by sensitive animals are part of a predator–prey pattern (Feder, 1959, 1963; Margolin, 1964a, b; Montgomery, 1967).

The active principle appears to be liberated from the epidermis of the tube feet (Feder, 1963; Feder & Lasker, 1964) and a sensitive mollusc can detect the presence of a starfish or an extract of starfish in the environment by both contact and distance chemoreception (Feder & Arvidsson, 1967; Montgomery, 1967).

An extract containing the active principle in an apparently stable form can be obtained simply by collecting the copious exudate from frozen starfish at room temperature. Studies on the nature of the active principle in such extracts of *Pisaster ochraceus* (Feder & Lasker, 1964) and of *Asterias rubens* and *Marthasterias glacialis* (Feder & Arvidsson, 1967) have involved the effects of organic solvents, heat, dialysis and gel-filtration. The results suggest that the activity is adsorbed or masked by protein. In contrast, Hashimoto (1967) has recently isolated and implicated a high-molecular weight lipoprotein as the active principle in *Asterias amurensis*.

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* Visiting Research Fellow, University of Aberdeen, 1966–67. Supported in part by National Science Foundation grant GB-2520 to Dr. Howard M. Feder. Permanent Address: U.S. Bureau of Commercial Fisheries, Fishery-Oceanography Center, La Jolla, California, U.S.A.

The purification and identification of the chemical nature of any biologically active molecule depends largely on reliable bio-assay procedures. In the present study, this assay must also accurately reflect the results obtained by the response of the intact animal. For this reason, a very sensitive and semi-quantitative bioassay was developed using the withdrawal response of the foot-muscle of intact *Buccinum undatum* to threshold amounts of active material. In this report we show that saponin-like compounds are the major active principle in extracts of *A. rubens* and *M. glacialis* and that their effects on *Buccinum* can be imitated by other surface-active agents.

MATERIALS AND METHODS

Animals

A. rubens, *M. glacialis* and *B. undatum* were obtained from the laboratory of the Scottish Marine Biological Association, Millport, Isle of Cumbrae. The starfish were collected from the estuary of the River Clyde in the summer and autumn and were stored at −20°C until required. *B. undatum* were dredged from areas around Millport and were maintained in a sea-water aquarium at 10°C.

Chemicals

Plant saponin was obtained from British Drug Houses Ltd., Poole, Dorset. Asterosaponins A and B (Yasumoto *et al.*, 1966) were a gift from Dr. J. D. Chanley, Mount Sinai Hospital, New York. Holothurin (Chanley *et al.*, 1960) was a gift from Dr. M. Stempien, Osborn Laboratory of Marine Sciences, New York. Triton X-100 (average molecular weight about 600) and Tween 80 were obtained from the Sigma Chemical Company, London. Lissapol N from Imperial Chemical Industries Ltd., Dyestuffs Division, Manchester. Sodium deoxycholate (enzyme grade) from Mann Research Laboratories, New York. Sodium taurocholate from Koch-Light Laboratories, Colnbrook. Heparin from Evans Medical Ltd., Liverpool. Blue Dextran 2000 (average molecular weight 2×10^6) and Sephadex G-75 from Pharmacia Ltd., London. Silica gel without binder (grade DO, "Camag") from Griffin & George Ltd., Middlesex.

Isolated radula muscle preparation and bioassay procedure

Because starfish extracts have been shown to initiate *Buccinum* radula muscle contraction (Fänge, 1963) we compared this reaction with those of the intact animal. The isolated *Buccinum undatum* radula muscle complex (odontophore apparatus) was prepared according to the method of Fänge & Mattisson (1958). As modified by Feder & Arvidsson (1967), the bio-assay procedure involves recording muscle contractions isometrically on a slowly moving smoked drum (4 mm/min). Our technique differed only in the use of a larger water bath (40 ml) to contain the suspended muscle in artificial sea water (Pantin, 1946; for details, see Lockwood, 1961) at 16° ± 0·5°C. Finally we compared active preparations by determining the range of concentration which either just elicited or failed to elicit a contraction of the muscle (range of threshold concentration). The threshold concentration of active substance varied in different muscles and indeed varied for the same muscle during the period it was in use for the bio-assay. For this reason a stock solution of the appropriate starfish extract was frozen at $-20°C$ in 1 ml amounts. Of this standard solution 10 μl was defined as one unit of activity. A thawed sample was used for 12 hr and was discarded after use.

The threshold for the muscle was determined with the standard solution immediately before determination of the threshold for a volume of the test solution. After each determination the muscle was washed three times with artificial sea water and allowed to relax to the original base line (about 30 min).

Bio-assay procedure using intact Buccinum

Prior to bio-assay, animals were placed in individual shallow trays containing sea water 1–1·5 cm deep. After 15 min, the tip of a 100 μl pipette was gently placed on the bottom of the container, about 2 mm from the exposed dorso-lateral muscle (Fig. 1), and 50 μl of sea water allowed to run out of the pipette. If the snail did not react to this control, the response to 20 μl of a test solution was noted. Active material in low concentration caused a mild contraction or "dimpling effect" at the edge of the foot-muscle followed by an immediate withdrawal of the foot-muscle at the point of application, culminating in the animal's moving away and twisting its shell (Fig. 1a–d). In order to compare the effects of various substances (Tables 2, 3 and 4) the range of threshold concentration which either just elicited or just failed to elicit the "dimpling effect" was determined for any single substance. In each assay, the activity of an individual substance and the standard solution was tested against at least four snails.

Semi-quantitative assay of haemolytic activity

Citrated human blood was washed by centrifugation with 0·9% (w/v) NaCl until the supernatant solution was clear and colourless. Two ml of packed cells were diluted to 200 ml with 0·9% (w/v) NaCl. Five ml portions were taken for assay, and up to 100 μl of test or standard solution were added for each assay. The suspensions were incubated at 20°C for 2 hr, centrifuged and the extinction of the clear red supernatant solution measured at 590 mμ in 1 cm cells. A solution of plant saponin (1 mg/ml) served as a standard. In the range 30–90 μl of standard solution, the extinction at 590 mμ was approximately proportional to the amount of standard saponin added. One unit of activity was defined as the amount of haemolytic material which caused the same degree of haemolysis as 1 mg of plant saponin.

Preparation of extract

Frozen starfish were allowed to thaw at 10°C and the exudate collected over a period of 12–15 hr.

Bulk fractionation of extract

All subsequent purification procedures were carried out at 4°C. Solid ammonium sulphate was added slowly to the exudate to give 60 per cent saturation (Dixon, 1953) and the mixture stood for 2–3 hr. The suspension was centrifuged at 2200 *g* for 45 min and the sediment resuspended in distilled water. A solution of 0·1 M-sodium bicarbonate was added slowly to raise the pH to 6–7, and phosphate buffer pH 7·0 was added to a final concentration of 0·05 M. The volume of the solution was half that of the original exudate.

An equal volume of 95% ethanol was added slowly and after 30 min the suspension was centrifuged at 2200 *g* for 45 min. The sediment was resuspended in 95% ethanol–water (1 : 1 v/v) and again centrifuged. The ethanol extracts were combined and evaporated under reduced pressure at 20°C to a final volume which was about one-tenth of the original exudate. The extract was dialysed against distilled water to remove salts and residual ethanol.

Gel filtration

10 ml of ethanol-soluble material from the bulk fractionation procedure (Table 1) were evaporated to dryness under reduced pressure at 20°C and the resulting material redissolved in 2·5 ml distilled water. This solution was centrifuged to remove a trace of insoluble material and was applied to a column of Sephadex G 75 (83 cm × 1·8 cm) previously equilibrated in distilled water adjusted to pH 7. The column was eluted with distilled water adjusted to pH 7, and 5 ml fractions were collected.

The column was later calibrated with a mixture of Blue Dextran and α, ϵ-di-(dinitrophenyl)-lysine. All operations were carried out at 4°C.

Extraction with butanol

Equal volumes of exudate and 95% ethanol were mixed and after a period of 30 min the mixture was filtered through fluted filter paper. The filtrate was evaporated at 20°C under reduced pressure to one-fifth to one-tenth the original volume of exudate. The solution, or the ethanol soluble material from the bulk fractionation (Table 1), was extracted three times with a volume of water-saturated butanol equal to half the volume of the aqueous solution. The butanol layers were combined and shaken with ether and distilled water as described by Yasumoto *et al.* (1964). By this means all the activity (foot-muscle bio-assay) was transferred to the aqueous phase. Water was removed by evaporation under reduced pressure and the crude saponin-like material was washed with acetone and finally with ether.

Paper and thin-layer chromatography

Chromatography of saponins was carried out using Whatman 3 MM paper and isopropanol : water (160 : 40 v/v) as solvent. To detect sugar components, 5–15 mg of saponin were hydrolysed in 2 ml of 2 N-HCl at 100°C for 2 hr. The insoluble steroid aglycones were removed by filtration and acid was removed *in vacuo* at 20°C. Chromatography of sugar components was carried out using Whatman No. 1 paper and either ethyl acetate : pyridine : water (10 : 4 : 3 by vol.) or butanol : pyridine : water (10 : 3 : 3 by vol.) as solvent. Authentic samples were used as markers.

Thin-layer chromatography of saponins or steroid aglycones was carried out on a silica-gel support (Grade DO, Camag) using one of the following solvents systems (Table 2). Solvent A, upper phase of the system butanol : ethylacetate : water (4 : 1 : 2 by vol.). Solvent B, butanol : acetic acid : water (12 : 3 : 5 by vol.). Solvent C, chloroform : methanol : water (188 : 12 : 1 by vol.). Solvent D, dichloromethane : acetone (130 : 70 v/v).

Saponins and steroid aglycones were detected by spraying developed chromatograms with either a 10% solution of phosphotungstic acid in ethanol (Smith, 1960) or a 25% solution of trichloracetic acid in chloroform (Heftmann & Hayden, 1952). Sugars were detected on paper by spraying with the standard aniline hydrogen phthalate reagent.

RESULTS

As judged by the assay involving the isolated radula muscle, preliminary experiments indicated that the activity in the extracts of both *A. rubens* and *M. glacialis* was essentially non-diffusible when dialysed against distilled or sea water at 4°C for 24 hr. It was partly destroyed by heating (100°C for 15 min) and by treatment with the protease preparation, Pronase (pH 8·6, 30°C for 2 hr). This suggested that a protein or polypeptide was an essential feature for activity but subsequent work showed that the active principle was a saponin-like molecule which, for the isolated muscle but not for the whole animal assay, required the active molecule to be in the form of a protein complex for the full expression of its activity.

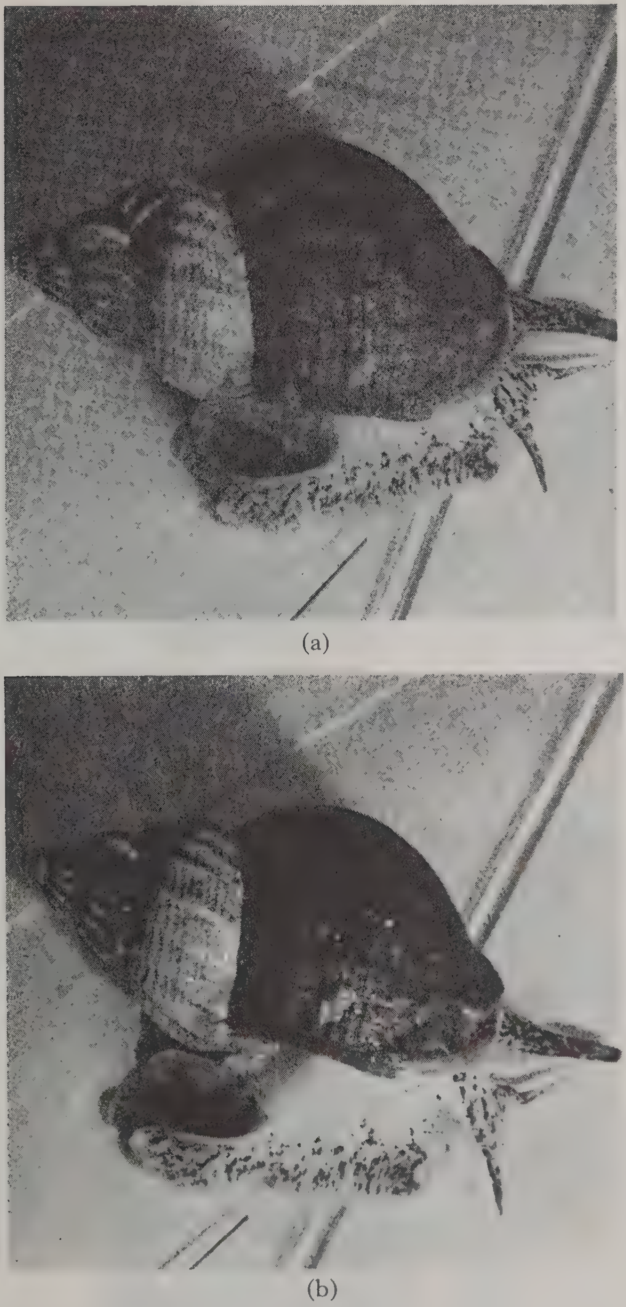
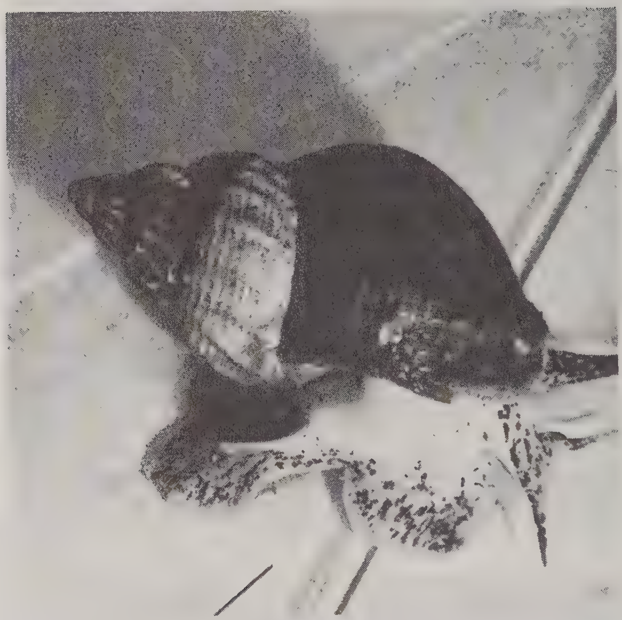


FIG. 1. The response of *B. undatum* to extracts of the starfish *A. rubens.* (a) Quiescent animal, showing tip of pipette resting on base of transparent container, 3 mm from the edge of foot muscle. Note position of animal relative to the external solid rod on which the tank was supported; (b) 50 μl of extract was run slowly from pipette and the response of the animal is shown 5 sec after the extract was added; (c) response of animal 10 sec after extract was added; (d) response of animal 15 sec after extract was added. Note movements of snail relative to the marker bar over the 15-sec period.



(c)

(d)

TABLE 1—BULK PURIFICATION OF ACTIVITY FROM AN EXTRACT OF *A. rubens*

Material	Dry wt. mg	Activity radula muscle assay			Haemolytic activity		
		Units	Units/mg dry wt.	%	Units	Units/mg dry wt.	%
Original extract (150 ml)	8700	15,000	1·7	100	800	0·09	100
60% sat. $(NH_4)_2SO_4$, supernatant	—	< 700	—	< 5	—	—	—
60% sat. $(NH_4)_2SO_4$, precipitate	—	11,000–12,000	—	70–80	—	—	—
50% (v/v) ethanol soluble fraction	420	6000–10,000	14–24	40–66	530	1·2	66
50% (v/v) ethanol insoluble fraction	850	< 300	—	< 2	—	—	—

— signifies value not determined.

TABLE 2—COMPARISON OF PROPERTIES OF ECHINODERM SAPONINS

Source and material	R_f thin-layer chromatography of saponin		R_f thin-layer chromatography of aglycone		Initial colour with phosphotungstate (10 min at 110°)	Sugars obtained after acid hydrolysis of saponin	Range of threshold concentration foot-muscle bio-assay	
	Solvent A	Solvent B	Solvent C	Solvent D			μg	μmole §
M. glacialis								
Saponin 1	0·05	0·29	0·26	0·38	Orange-brown	Fucose, quinovose, glucose, (trace of xylose)*	1–3*	About 0·002
Saponin 2	0·09(0·12†)	0·32	0·22	0·30	Green	Fucose, quinovose, glucose	1–3	
A. rubens								
Saponin 1	0·05(0·13‡)	0·29(0·35‡)	0·26	0·38	Orange-brown	Fucose, quinovose (traces of glucose, xylose and galactose)	2–4	
A. amurensis								
Saponin A	0·05	0·29	—	—	Orange-brown	Fucose, quinovose		
Saponin B	0·02	0·24	—	—	Orange-brown	Fucose, quinovose, xylose, galactose		
Actinopyga agassizi								
Holothurin of sea-cucumber	—	0·57(0·44‡)	—	—	Yellow	—	60–80	About 0·06

* Mixture of saponin 1 and 2.
† Minor or trace component, yellow colour with spray reagent not detectable in solvent B.
‡ Minor or trace component.
§ Assuming a molecular weight of 1200.

Active principle of A. rubens

The activity in the crude extract behaved like a protein when subjected to the normal bulk fractionation procedures (Table 1), and resulted in a twelve- to fifteen-fold purification together with a reasonable recovery of activity. Subsequently, a further degree of purification was attempted by gel-filtration on Sephadex G 75. An unexpected result was that high-molecular weight material (Fraction 1, Fig. 2) was completely devoid of activity towards the isolated radula muscle. Assays of the subsequent fractions showed that a low-molecular weight haemolytic material (fraction 2, Fig. 2), eluted before the coloured marker (α, ε-di-(dinitrophenyl)-lysine, molecular weight 514, contained some activity towards the isolated radula muscle in an amount corresponding to a small fraction of the total applied to the column. However, when equal amounts of fractions 1 and 2 were mixed before addition, the muscle responded with a strong contraction (Fig. 3). Subsequent assays established that more than 90 per cent of the activity originally applied to the column could be accounted for by the recombination of the separated fractions.

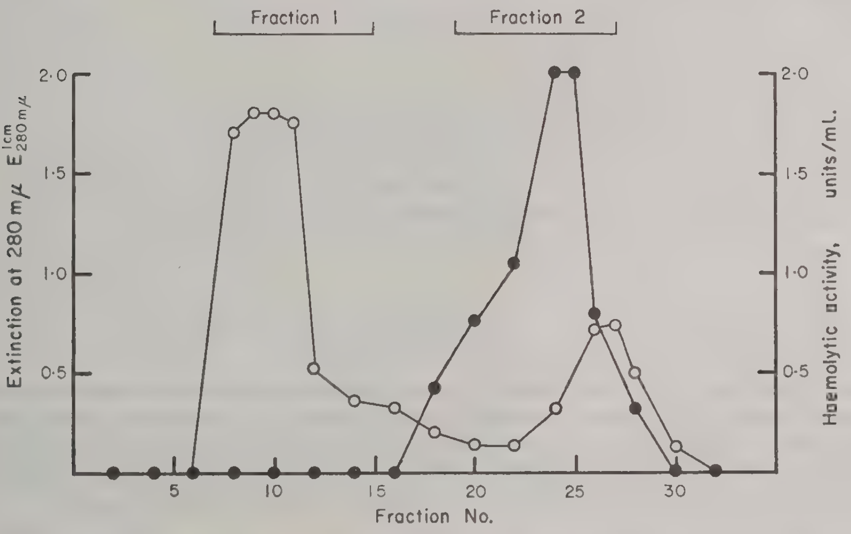


Fig. 2. Gel-filtration of an ethanol-soluble fraction. Details in Materials and Methods section and Table 1. ○—○—○, extinction at 280 mμ. ●—●—●, haemolytic activity per ml. Fraction volume, 5 ml. The retention volume of a high-molecular weight Blue Dextran marker was 50 ml and that of α, ε-di-(dinitrophenyl)-lysine was 140 ml.

In contrast, when tested by the intact animal assay, fraction 2 on its own was highly active. Fraction 1 was devoid of activity and it did not have any detectable potentiating effect on the activity of fraction 2.

These results show that the *in vitro* muscle assay is not, in this instance, a true measure of the response of the intact animal. For example, a solution containing 10 μg dry weight of fraction 2 effected an immediate and violent response in the intact snail whereas more than 200 μg was necessary to achieve even a slight contraction in the muscle assay after a time lag of several minutes. On the assumption that the active principle is the same for both assay systems, it seemed possible that the essential role of protein to the isolated muscle system was that of an inert and non-specific carrier. However, attempts to potentiate the effect of fraction 2 on the isolated muscle system by various proteins such as bovine plasma albumin, human serum, poly L-lysine and an egg phosphoprotein were not successful.

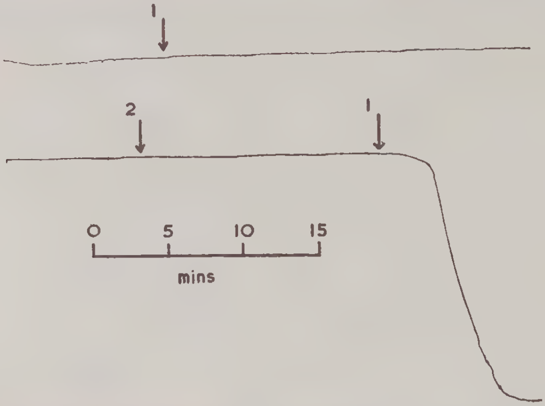


FIG. 3. Effect of fractions obtained by gel-filtration on the isolated radula muscle. Upper tracing: the lack of response to the arrowed (1) addition of the high-molecular weight fraction. Lower tracing: the lack of response to the arrowed (2) addition of the haemolytic fraction and the contraction of the muscle to the subsequent arrowed (1) addition of the high-molecular weight fraction.

The active principle was not retained by percolating fraction 2 through a column of Dowex 50 in the H^+ form and eluting with water. The eluate did not react with ninhydrin so that peptides and other amines were not involved. Paper chromatography of the eluate with isopropanol–water as solvent indicated that one major band ($R_f = 0{\cdot}3$–$0{\cdot}5$) was present together with traces of at least four other steroid components as judged by either the trichloroacetic acid–chloroform or phosphotungstic acid spray reagents. Assays of the material eluted from strips of untreated chromatograms cut at right-angles to the direction of solvent flow showed that both the haemolytic activity, and the activity by foot-muscle bio-assay was associated with the major "steroid" band present in that section of the paper corresponding to an R_f range of 0·3–0·5. Although thin-layer chromatography of this material, designated saponin 1, indicated the presence of a minor or trace steroid contaminant (Table 2), these results suggest that a large part if not all of the activity of the starfish extract towards the intact snail can be attributed to this saponin-like substance or substances.

The same substance can also be obtained relatively easily by removing most of the protein from the crude extract with ethanol and extracting a concentrated solution of the supernatant with butanol as described in the Materials and Methods section. Further details of the chromatographic behaviour and other properties of saponin 1 are given in Table 2 and this direct comparison would indicate that saponin 1 closely resembles and may be identical with the asterosaponin A which was isolated from Pacific starfish and partly characterized by Yasumoto & Hashimoto (1965).

Active principle of M. glacialis

The active principle in extracts of *M. glacialis* behaved in an entirely similar manner to that of *A. rubens* when subjected to the bulk fractionation procedures for proteins (Table 1), gel-filtration (Fig. 2), extraction of the protein-free crude extract with butanol and removal of inert peptides and other amines by Dowex 50.

Paper chromatography with isopropanol–water as solvent also showed that the haemolytic activity and the activity towards the foot-muscle bio-assay could be identified with two poorly separated major saponin-like components. Saponin 1 ($R_f = 0{\cdot}4$–$0{\cdot}55$) gave a brown colour with phosphotungstate while saponin 2 ($R_f = 0{\cdot}55$–$0{\cdot}65$) gave a green colour. The results of thin-layer chromatography (Table 2) of saponin 1 of *M. glacialis* would indicate that it is chemically similar if not identical with that of saponin 1 of *A. rubens* and asterosaponin A of Yasumoto & Hashimoto (1965).

A small quantity of saponin 2 was isolated free from saponin 1 by elution from a strip corresponding to an R_f of 0·6–0·65 cut at right-angles to the direction of solvent flow from a developed but otherwise untreated paper chromatogram (Whatman 3 MM paper, 40 mg material applied as a streak, 150 cm in length). In its chemical, but not in its biological properties, saponin 2 appears to differ quite markedly from other starfish saponins described here (Table 2) and by Yasumoto & Hashimoto (1965). The presence of a minor or trace amount of a contaminant steroid was however demonstrated by thin-layer chromatography with Solvent A but not with Solvent B.

Response of the foot-muscle of the intact Buccinum *to saponins and other substances*

Under the standard conditions of bio-assay, the intact snail responded within 5 sec by a slight contraction or "dimpling effect" of the foot-muscle (Fig. 1) at the point of application of a minimum effective dose of saponin 1 (2–3 μg, 20 μl) from *A. rubens*, or a mixture of saponins 1 and 2 from *M. glacialis* (Table 2). The response to a higher dose (400–500 μg, 20 μl) was equally rapid and resulted in a massive contraction of the muscle starting and continuing from the point of application of the test dose. The snail toppled over and almost the whole body emerged from the shell in a violent series of convulsive and twisting movements. This violent reaction did not appear to cause any obvious permanent damage to about 75 per cent of the snails tested; the survivors, if required, responded to a test dose after a few days' rest.

These haemolytic starfish saponins are freely soluble in water (>100 mg/ml) and an aqueous solution, when shaken, produces a copious and stable foam. For this reason, the range of threshold concentration required to elicit the "dimpling effect" on the foot-muscle of the intact snail was determined for a range of other

TABLE 3—ACTIVITY, FOOT-MUSCLE BIO-ASSAY OF SURFACE-ACTIVE AGENTS

	Substance tested in sea water (pH 7·5)	Range of "threshold concentration" (μg)	(μmole)
Non-ionic detergents	Octylphenoxypolyethoxyethanol (Triton X-100)	1–2	0·002–0·003
	Nonylphenoxypolyethoxyethanol (Lissapol N)	1–2	—
	Polyoxyethylene sorbitan mono-oleate (Tween 80)	3–5	—
Cationic detergents	Cetyltrimethylammonium chloride	3–5	0·01–0·015
	Cetylpyridinium chloride	10–14	0·03–0·04
Anionic detergents	Sodium deoxycholate	30–40	0·07–0·1
	Sodium taurocholate	About 150	About 0·3
	Sodium lauryl sulphate	About 200	About 0·7

surface-active agents. The most effective in this respect (Table 3) were those which contain either a non-ionic or a cationic (positively charged, fully ionized at the pH of sea water) hydrophilic group in the molecule. In contrast, the foot-muscle was not nearly so sensitive, under the same conditions, to anionic detergents such as lauryl sulphate, taurocholate (Table 3) and holothurin (Table 2), which all contain a fully ionized sulphate anion hydrophilic group. The intermediate position of deoxycholate may be explained on the basis that this anionic detergent (carboxyl group, pK about 6–7) will only be partially ionized at the pH of sea water.

The high activity of the polymers, Triton X-100 and Tween-80 is comparable on a weight basis to the starfish saponins, and is of the same order when a comparison is made on a molar basis. At a higher concentration (400–500 μg) both Triton X-100 and cetyltrimethyl ammonium chloride have also been found to induce the involuntary convulsive effects on the intact snail. For these reasons it is suggested that the action of both these detergents and the starfish saponins can be attributed to their surface-active properties exerting an effect at the same loci on the snail's foot-muscle.

The relative activity of a variety of compounds, including a non-surface active cation (choline) and polyanion (heparin) on the foot-muscle assay is given in Table 4.

TABLE 4—ACTIVITY, FOOT-MUSCLE BIO-ASSAY OF VARIOUS SUBSTANCES

Substance, tested in sea water (pH 7·5 except where otherwise noted)	Range of "threshold concentrations" (μg)	(μmole)
$ZnSO_4$ (pH 6)	About 100	0·6
$CaCl_2$ (pH 6·6)	About 400	4·0
NH_4Cl (pH 6·6)	About 500	10·0
Na_2SO_4	About 700	5·0
$MgCl_2$	About 700	8·0
Acetylcholine chloride	About 100	0·6
Choline bromide	About 400	2·0
Heparin	About 200	—
Glucose, glycine, histamine Sodium chloride	>1000	—
Sea water adjusted to pH 3 with HCl	No effect	—

DISCUSSION

The present work indicates that the principal substance in extracts of *A. rubens* and *M. glacialis*, which can elicit an escape response in *B. undatum*, is a saponin-like molecule which exists as an equilibrium mixture of free saponin and its protein complex. Saponins are known to aggregate in solution to form micelles that dialyse slowly through a cellophane membrane. This behaviour together with the known properties and stabilities of complexes formed between proteins and steroid derivatives (Westphal, 1961) may provide a satisfactory basis to account for some of the results of previous studies (Feder, 1956; Feder & Lasker, 1964; Feder & Arvidsson, 1967) on the active principle present in extracts of starfish.

The early and disconcerting observation that the isolated radula muscle requires both the protein and the saponin-like fractions (Fig. 2) for activity (Fig. 3), leaves the respective functions, particularly that of the protein, to be explained. The present results would indicate that the protein is unlikely to function as an inert and non-specific carrier and it remains possible that a polypeptide is the active principle in this instance whose entry into the muscle is facilitated by the surface-active properties of the saponin. Whatever the correct explanation may be, we have shown here that the muscle assay does not accurately reflect the behaviour of the intact animal except when the test substance is an unfractionated protein–saponin complex. At the same time this complex will also elicit the contraction of a mammalian smooth muscle such as the guinea pig ileum (unpublished results). This indicates that further studies are desirable on this interesting invertebrate type of "smooth muscle" as an extension to the valuable studies made by Fänge & Mattisson (1958), Fänge (1963), Mattisson & Arvidsson (1966) and Feder & Arvidsson (1967).

The first identification of steroid saponins in tissues other than green plants was made independently by Nigrelli (1952) and Yamanouchi (1955) during studies on a toxic principle present in sea cucumbers. Subsequent work on echinoderms established that a number of saponins are present in sea cucumbers (Chanley *et al.*, 1960; Yasumoto *et al.*, 1967) and that others of a differing composition both with regard to the nature of the steroid aglycone and the sugar moieties were found in starfish (Yasumoto & Hashimoto, 1965; Rio *et al.*, 1965). In a recent survey of starfish occurring in Japanese waters, Yasumoto *et al.* (1966) have concluded that the same two principal saponins were present in all starfish examined. A direct comparison (Table 2) would indicate that both the saponin of *A. rubens* and probably saponin 1 of *M. glacialis* from Scottish waters are very similar if not identical with those isolated from Pacific starfish. At the same time, saponin 2 of *M. glacialis* is quite distinct and does not appear to have been described previously. A further and more definitive analysis of these starfish saponins, particularly on the nature of the steroid aglycone, is in progress.

Although a variety of toxic and other pharmacological effects have been ascribed to the hemolytic saponins of starfish (Yasumoto *et al.*, 1964; Rio *et al.*, 1965) their identity as the causative agent of the mollusc avoidance reaction has not, as far as we are aware, been previously noted.

The mode of action of surface-active bactericides (Sexton, 1953) has generally been ascribed to their reaction with lipid–water interphases resulting in a progressive disorganization of outer membranes and structures of cells which control osmotic equilibrium. This type of reaction will also occur with all surface cells and membranes when saponins and other surface-active agents act on the foot muscle of *Buccinum*, but for the following reasons it is unlikely to be the primary cause of the observed response of the snail: the foot-muscle responds immediately to a minute dose of a few microgrammes, and the involuntary and convulsive response to an increased dose involves the body of the snail and occurs equally rapidly. Accordingly, it is suggested that the primary cause of the response to saponin in these experiments is their reaction with or damage to (by detergent or surface-active properties) chemosensory cells of nervous origin in or near the surface epithelium of the foot-muscle. Damage to chemosensory cells need not permanently affect the subsequent well-being of the animal since these cells are usually held (Hodgson, 1965) to be regenerated rapidly. In this connection, it remains possible that the active lipoprotein isolated from *A. amurensis* by Hashimoto (1967) may contain a surface-active component such as an unsaturated fatty acid or phospholipid derivative as the active principle.

The present results do not preclude the possibility that other structures of *Buccinum* may contain chemosensory cells sensitive to extracts of starfish. Indeed, studies on the escape response of the gastropod *Tegula funebralis* from which various structures had been removed would indicate that the osphradium acts as a sensitive chemoreceptor to extracts of *Pisaster ochraceus* (Burke, 1964). It is possible to monitor nervous impulses in the supra-oesophageal ganglion which originate by chemical stimuli of the osphradium of *Buccinum*, but in this electrophysiological study (Bailey & Laverack, 1963) only a very limited range of compounds were tested for activity. Irrespective of speculations as to the loci and exact mechanism of action, the results reported here would suggest that the presence of certain non-ionic or cationic detergents in the natural environment may constitute a previously unsuspected hazard to *Buccinum* and possibly other molluscs.

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Production of Sea Lamprey Larvae from Nests in Two Lake Superior Streams

Patrick J. Manion

Production of Sea Lamprey Larvae from Nests in Two Lake Superior Streams[1]

INTRODUCTION

The life history of the landlocked sea lamprey, *Petromyzon marinus*, has been described by several authors, the two most recent of which are Applegate (1950) and Wigley (1959). The only information on the production of larvae from nests of the sea lamprey was reported by Applegate (1950), who counted the larvae from three nests in the Ocqueoc River, a tributary of Lake Huron. The present report presents data on the hatching success of sea lamprey larvae from 19 nests in two small tributaries of southern Lake Superior and indicates greater production per nest than that recorded by Applegate.

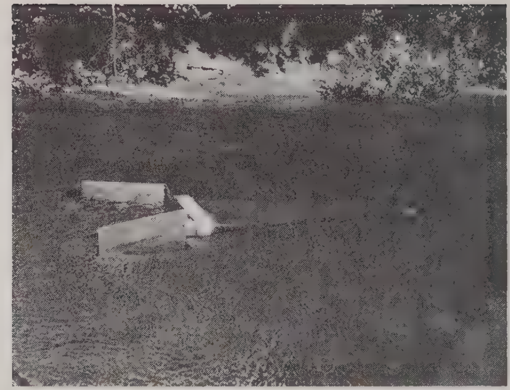

FIGURE 1.—A trap for collecting sea lamprey larvae.

HABITAT DESCRIPTION AND SAMPLING TECHNIQUES

Studies were conducted by personnel of the U. S. Bureau of Commercial Fisheries on the Little Garlic River, Marquette County, Michigan, and on the Traverse River, Keweenaw County, Michigan. Both rivers are small; they vary in width from 6 to 30 ft and average 15 inches in depth. Stream flow during the sea lamprey spawning season is approximately 8 ft^3/sec.

Larvae were collected from six nests in June 1963 and eight nests in July 1965 in the Little Garlic River and from five nests in July 1966 in the Traverse River. The study nests were sampled 13 to 15 days after egg deposition. Sampling dates were based on embryological stages described by Piavis (1961) and on Applegate's (1950) report that larvae leave the nest 18 to 21 days after completion of spawning by the parent fish.

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[1] Contribution No. 374 of the Ann Arbor Biological Laboratory, U. S. Bureau of Commercial Fisheries.

TABLE 1.—*Number of sea lamprey larvae hatched in single (S) and double (D) nests*[1] *in the Little Garlic and Traverse Rivers*

Little Garlic River						Traverse River		
June 1963			July 1965			July 1966		
Day	Nest type	Larvae	Day	Nest type	Larvae	Day	Nest type	Larvae
24	S	4,192	6	S	3,058	6	S	3,346
24	S	4,563	6	S	3,821	6	S	2,559
24	S	3,621	6	D	8,818	6	S	3,111
24	S	3,740	12	D	6,465	6	D	5,109
25	D	9,816	21	D	6,703	6	D	5,304
29	D	10,545	21	D	7,488			
			21	S	1,763			
			21	S	1,864			
Average								
Single		4,029			2,627			3,005
Double		10,181			7,369			5,207

[1] Single nests were those used by one pair of spawning lampreys and double nests by two pairs of lampreys.

Embryological development of the larvae from both rivers was similar to that described by Piavis, and none had progressed beyond the gill-cleft stage (15 to 17 days after egg fertilization). Piavis (1961) found that larvae do not develop definite swimming patterns until the gill-cleft stage and do not start to burrow until 17 to 33 days after egg fertilization.

Larvae were counted only in nests where the number of spawning adults was known and where spawning was completed. Nests used by one pair of adults were termed single and those used by two pairs were double. Actual counts were made of the larvae hatched from each nest.

The trap used to collect larvae from the nests consisted of a rectangular plywood funnel, 24 inches wide by 10 inches high, with a 24 × 16 inch aluminum wing on either side (Figure 1). A 6-foot plankton net (silk No. 20, 0.076-mm mesh) was attached to the funnel.

The trap was placed below the downstream lip of the nest, and the funnel was placed on the stream bottom. The aluminum wings extended upstream on either side of the nest, and the plankton net extended downstream. Cracks and crevices under the funnel and wings were filled with sand to prevent escapement of larvae.

After placement of the trap, the nest was dismantled. Large rocks (½ to 4 inches in diameter) were removed from the downstream crest of the nest and washed in front of the trap to remove the larvae; larvae left in the nest were dislodged by carefully sifting the gravel and sand through the fingers. The water current carried the larvae downstream into the trap, from which they were periodically removed through the rear opening and preserved in 3% formalin. This procedure was continued until no more larvae could be collected.

Possible sources of bias in the estimation of "hatching success" (i.e., successful development of the larvae to the gill-cleft stage) were the drift of eggs from the nest and predation by fish. Eggs were observed to drift over the crest of the nest during the spawning act, but the numbers were not determined. Logperch (*Percina caprodes*) and small rainbow trout (*Salmo gairdnerii*) ate eggs in and near the nest during the spawning act and larvae when the nest was sampled.

HATCHING SUCCESS

Of the 19 nests examined, 11 were single and 8 were double (Table 1). The average production of larvae was higher in nests examined in June 1963 than in those studied in July 1965 and 1966. The mean number of larvae removed per nest from the Little Garlic River was 4,029 from single nests and 10,181 from double nests in June 1963, and 2,627 from single nests and 7,369 from double nests in July 1965. In July 1966, the average yields in three single and two double nests in the Traverse River were 3,005 and 5,207 larvae, respectively.

Production of larvae varied from 1,763 to 10,545 per nest for all samples taken, in the 3 years, from both rivers. The mean number of larvae from single nests was 3,240 and from the double nests, 7,531; double and single nests combined averaged 5,047 larvae per nest.

Estimates of hatching success were based on fecundity estimates of Applegate (1950). Although the 27 females in this study were not measured, I assumed that their average lengths equaled those for females captured at electric barriers during spawning runs in tributaries along the south shore of Lake Superior in the same years, 16.9 inches in 1963 and 1965 and 16.1 inches in 1966. Females 16.9

and 16.1 inches long had a potential egg production of approximately 58,700 and 52,500 eggs, respectively. Average production of larvae per female was 4,560 in 1963, 3,332 in 1965, and 2,776 in 1966. Hatching success of the eggs, therefore, was estimated at 7.8% in 1963, 5.7% in 1965, and 5.3% in 1966 (average was 6.3% for the 3 years). Hatching success was significantly higher than that determined by Applegate (1950), who reported hatching percentages of 0.4, 0.7, and 1.1 in three single nests in the Ocqueoc River, Lake Huron.

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Patrick J. Manion

U. S. Bureau of Commercial Fisheries
Biological Station
Marquette, Michigan

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Cooperative Study of the Kuroshio and Adjacent Regions

The Cooperative Study of the Kuroshio and Adjacent Regions (CSK) is a cooperative international undertaking under the auspices of the Intergovernmental Oceanographic Commission (IOC) of Unesco and the Indo-Pacific Fisheries Council of FAO. The CSK area extends from 160°E longitude to the mainland of Asia and from 4°S to 47°N latitude. The first field work was in the summer of 1965.

The CSK is coordinated by an International Coordinating Group (ICG), consisting of the national coordinators and assistant national coordinators of the 11 member countries. K. Wadati (Saitama University) serves as International Coordinator, and J. Marr (U.S. Bureau of Commercial Fisheries, Honolulu) serves as Assistant International Coordinator for Fisheries. The Secretariat is provided by the IOC.

The ICG/CSK Fifth Meeting was held at the East-West Center, University of Hawaii, Honolulu, on May 3–4, 1968. The participating countries included China, Japan, Korea, Philippines, Singapore, Thailand, United Kingdom (Hong Kong), United States, and USSR. Indonesia and Viet Nam were not represented. The meeting was preceded by a symposium, April 29 to May 2, in which 47 individuals from nine countries participated. There were 75 papers presented: 21 on oceanography, 29 on fisheries, 15 on plankton, and 10 by title only. The Convenor of the symposium was J. Marr. He will also serve as editor of the publications based on this Symposium; one volume will contain a summary report and abstracts of papers, and a second volume will give the papers in full.

Of particular interest in physical oceanography were the results reported on the Kuroshio-Oyashio front (especially the eddies associated with it) and on a subtropical countercurrent. Work relating to the Kuroshio-Oyashio front was reported by R. Barkley (U. S. Bureau of Commercial Fisheries, Honolulu), T. Ichiye (Lamont Geological Observatory), A. Muromtsev (State Oceanographic Institute, Moscow), and M. Uda (Tokai University). Barkley had recently [*J. Mar'me Res.*, *26*(2), 83–104, 1968] suggested a kinematic model of the front consisting of a pair of von Kármán vortex streets arranged side by side. The system appears to be quasi-stationary, although the model involved an eastward displacement of about 50 cm $\sec^{-1}$. When Coriolis force is taken into account, this discrepancy is eliminated and the model conforms to observation.

Subtropical countercurrents between 20° and 25° latitudes had previously been postulated by K. Yoshida (University of Tokyo). The existence of such countercurrents in the North Pacific was verified by Yoshida, J. Masuzawa (Japan Meteorological Agency), Muromtsev, and Uda. They are best developed in winter and spring at surface velocities of the order of 10–20 cm/sec. Although it remains to be verified by future observations, a remarkable feature may be the existence of eastward flow in latitudinally separated bands.

A fuller account of the results of the symposium will be presented in *Science*.

At the ICG/CSK Fifth Meeting, it was decided that the synoptic surveys in the Pacific Ocean part of the CSK area will be continued through the summer of 1970. Although other kinds of observations have been taken, the emphasis in these cruises has been on physical oceanography. In contrast, survey cruises in the South China Sea will emphasize fisheries, although observations on physical oceanography will also be made. These cruises are just starting and will probably be continued beyond 1970. Other studies in physical oceanography recommended at the Fifth Meeting include (1) investigation of the subtropical countercurrent, (2) investigation, with special emphasis on transport, of the equatorial current and the Kuroshio upstream of Japan, (3) investigation of the southern route (southeast of Japan) of the Kuroshio and the influence of the Izu-Bonin ridge on the Kuroshio, (4)investigation of the coastal and interisland shelf areas of the western Pacific and the South China Sea, and (5) investigation of the area south of 20°N latitude (largely neglected until now owing to lack of ship time).

U. S. investigators who are planning work in the CSK area are urged to make their plans known to the U. S. National Coordinator, J. Marr, or the Assistant National Coordinator, T. Treadwell (Naval Oceanographic Office, Washington, D. C.).

It is obvious that important progress has been made in the understanding of the oceanography of the western Pacific and that some of this understanding is general enough to be of application elsewhere in the world. The results of the fishery studies will also be of great importance but will require somewhat more time to come to term. The most important aspect of the CSK may well prove to be the contacts established, the lines of communications opened and the experience gained in cooperative effort among the CSK countries.

John C. Marr
U. S. Bureau of Commercial Fisheries,
Honolulu, Hawaii 96812

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Hawaii

By JOHN C. MARR
Area Director
Bur. of Comm. Fisheries
Honolulu, Hawaii

LATE IN 1965 Governor John A. Burns of the State of Hawaii called a Governor's Conference on Central Pacific Fishery Resources. This Conference resulted in the first numerical estimates of the size of the unfished stock of skipjack tuna of the central Pacific. These estimates have lent new impetus to research on methods of improving and expanding the Hawaiian skipjack tuna fishery. The skipjack tuna fleet based in Hawaii has shrunk from 27 vessels operating in 1950 to only 16 vessels in 1968, despite the fact that there exists in the central Pacific Ocean this almost untouched resource of skipjack tuna whose potential annual yield lies in the hundreds of thousands of tons. By way of reference a 100,000 ton yield is estimated to be valued at perhaps $25 million to the fishermen, $62 million to the processor, and $100 million at the retail level. The fishing boats are faced with a critical manpower shortage. Moreover, they are undercapitalized and shackled by a powerful tradition of maintaining the status quo. The vessels are too small to venture farther than a few miles from the islands into areas where catch rates may be better. There is also the problem of poor survival qualities of the small anchovy used as baitfish in this fishery. The Bureau of Commercial Fisheries in Hawaii hopes to help sustain the present Hawaiian skipjack tuna fleet, retaining intact a cadre of skilled manpower, by reducing its dependence on the present bait and by a thorough analysis of its day-to-day operations. This pool of specialized skills and knowledge will be required if the skipjack tuna resource in the central Pacific is to be harvested from a Hawaiian base.

Landings of skipjack tuna—the mainstay of the Hawaiian commercial fishery—were estimated to be about 7.6 million pounds through August. Based on the relationship of the environment and availability of skipjack in Hawaiian waters, scientists at the Biological Laboratory, Honolulu, predicted in March 1968 that this year's skipjack landings would be less than the long-term average of 10 million pounds. Since about 53 percent of the yearly catch is taken during the summer, it seems likely that this prediction will come true and that the 1968 landings will be about 9 million pounds.

Longline catches of bigeye tuna, yellowfin tuna, and billfish are also below average so far this year. Through August, a combined total of about 875,000 pounds had been landed, as opposed to catches of about 1.2 million pounds by this time in previous years. Thus, it appears that the 1968 landings will fail to reach the average of about 1.7 million pounds.

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SCIENCE

Kuroshio

A symposium on the results of the "Cooperative Study of the Kuroshio and Adjacent Regions" (CSK) was held at the East-West Center, University of Hawaii, Honolulu, 29 April–2 May 1968. The CSK area extends from 160°E to the mainland of Asia and from 4°S to 47°N. Subject matter of the papers presented at the symposium included oceanography, fisheries, and plankton.

In oceanography most interest centered on a subtropical countercurrent, transport, and velocity in the Kuroshio, and frontal processes and eddies associated with the Kuroshio-Oyashio interface. Other papers dealt with such widely varied topics as fine-scale temperature profiles (as revealed by thermistor chain) in the Kuroshio, currents in Korea Strait, and bathymetry of the South China Sea.

The existence of a subtropical countercurrent, which had been postulated earlier by Yoshida (University of Tokyo) on the basis of transport computations from seasonal wind-stress distributions, was verified by Yoshida as well as by Masuzawa (Japan Meteorological Agency), Muromtsev (State Oceanographic Institute, Moscow), and Uda (Tokai University). This eastward-flowing current is believed to be a permanent or semipermanent feature in the latitudes of 20°N to 24°N, best developed in winter and spring. Surface velocities are of the order of 10 to 20 cm/sec. A remarkable feature, which remains to be verified by more closely spaced observations, appears to be the existence of banding; easterly flow apparently takes place in bands located between 21°N to 22°N, 24°N to 25°N, and 27°N to 28°N. Data from the Hawaiian Islands region and the Sargasso Sea also showed indications of easterly flows north of 20°N. These results lead Yoshida to expect, in conformity with his earlier computations, that easterly flows will be found between 20°N to 25°N and 20°S to 25°S in all the world oceans.

Information on transport and velocity at a number of geographic locations in the Kuroshio was presented by Chu (National Taiwan University), Nitani (Hydrographic Office of Japan), Nitani and Shoji (Hydrographic Office of Japan), Muromtsev, and Uda. Nitani, for example, finds the transport to be 30×10^6 m^3/sec east of Luzon, 40×10^6 m^3/sec east of Taiwan, and 45 to 50×10^6 m^3/sec south of Kyushu. Transport and velocity estimates were based primarily on geostrophic computations, although some GEK observations were made. The need was felt for direct current observations at subsurface levels.

The Kuroshio-Oyashio front, and particularly the eddies associated with it, received attention from Barkley (U.S. Bureau of Commercial Fisheries, Honolulu), Ichiye (Lamont Geological Observatory), Muromtsev, and Uda. Barkley had recently presented a kinematic model of the front, consisting of a pair of von Kármán vortex streets arranged side by side. Although his model explained many major features of the region, it did involve an eastward displacement of the system of about 50 cm/sec, whereas in reality the system appears to be quasi-stationary. By taking Coriolis force into account, this feature is overcome and the model conforms to observation. Predictions arising from the model suggest the design of field work to test the model. Attention was drawn by Uda to the relation between the distribution and abundance of certain fishes and whales and the location of the eddies.

On the subject of fisheries, attention was centered on demersal fisheries, particularly in the Sunda Shelf region, fishery oceanography, species synopses and systematics of anchovy, threadfin-bream, and lizard fish, and subpopulation identification of skipjack tuna and other fishes. Other papers dealt with such topics as the distribution and abundance of larval skipjack, tagging experiments on several species, and the association between tunas and floating objects.

The phenomenal development of the demersal fishery in the Gulf of Thailand, resulting from the introduction of appropriate new technology, was reported by Tiews (Bundesforschungsanstalt für Fischerei, Hamburg), Sucondhmarn (Department of Fisheries, Thailand), and Isarankura (Department of Fisheries, Thailand). The growth of the fishery has been so spectacular that it may now be considerably overcapitalized. Stock assessment studies are seriously handicapped by the lack of adequate catch and effort data and by the fact that the fisheries are based upon a large number of species. The demersal productivity of the Gulf of Thailand has proven to be much greater than was previously believed to be the case for tropical areas in general and for this area in particular. This productivity had led Tiews to estimate a rather startlingly high demersal productivity potential for Southeast Asia. As a consequence, Menasveta (Department of Fisheries, Thailand) reviewed all the available data on the demersal productivity of the Sunda Shelf. His results indicate that, while the productivity is not as high as suggested by Tiews, it is certainly higher than would have been believed 10 years ago. In connection with demersal fisheries, the need was felt for better catch and effort data and for stock assessment studies.

Various aspects of fishery oceanography were reported by Han and Gong (Fisheries Research and Development Agency, Korea), Hattori (Tokai Regional Fisheries Research Laboratory), Hirano and Fujimoto (Tokai Regional Fisheries Research Laboratory), and Uda. Uda's comments on the association of fishes and whales with the eddies of the Kuroshio-Oyashio have already been noted. Hattori presented interesting information on the distribution of fish larvae in a section across the Kuroshio south of southern Honshu. These data could be categorized in four groups: those species found only inshore of the Kuroshio, those found inshore and on the offshore side of the Kuroshio but not in between, those found throughout the entire section, and those found only in the offshore area.

Fishes of the genera *Nemipterus, Saurida,* and *Stolephorus* have not been studied comprehensively. As a result, their systematics and nomenclature and the distribution of individual species are not well known. Systematic works on these genera by Eggleston (Agriculture and Fisheries Department, Hong Kong), Shindo (Seikai Regional Fisheries Research Laboratory), and Ronquillo (Philippine Fisheries Commission), respectively, were welcome. Summaries of information or species synopses in the format of the Food and Agriculture Organization were presented by Isarankura for *Nemipterus hexodon,* by Nakamura (U.S. Bureau of Commercial Fisheries, Honolulu) for *Stolephorus purpureus*, and by Tham (University of Singapore) for *S. pseudoheterolobus.*

Data based on a serum esterase system examined by Fujino (U.S. Bureau of Commercial Fisheries, Honolulu) show that the skipjack tuna, *Katsuwonus pelamis*, from Japan, Okinawa, Marianas, and Palau are genetically distinct from those found in the Hawaiian Islands and in the northeastern tropical Pacific. There was no evidence suggesting the existence of more than one subpopulation in the western Pacific. The need was recognized for subpopulation studies for a number of species and the saury, *Cololabis saira*, and chub mackerel, *Rastrelliger brachysoma*, were identified in particular as presenting pressing problems.

In plankton, interest was primarily on distribution and distribution in relation to environment. Other subjects were discussed including systematics. Particular interest was shown in the charts of Yamazi (National Science Museum, Tokyo) showing the distribution and abundance of a large number of plankters.

Participating in the symposium were individuals from nine countries. The convenor of the symposium, John C. Marr (U.S. Bureau of Commercial Fisheries, Honolulu), will act as editor of the publications—a volume including a summary report and abstracts of papers to be published in the immediate future and the proceedings, including the papers in full, to be published as soon as possible.

The symposium was followed on 3–4 May by the fifth meeting of the CSK International Coordinating Group. Kiyoo Wadati (Saitama University) serves as the international coordinator and Marr as the assistant international coordinator for fisheries. The CSK is carried out under the sponsorship of the Intergovernmental Oceanographic Commission, UNESCO, and the Fisheries Department, FAO. Countries participating in the fifth meeting included China, Japan, Korea, Philippines, Singapore, Thailand, United Kingdom (Hong Kong), the United States, and the U.S.S.R. Absent were Indonesia and Viet Nam.

JOHN C. MARR

U.S. Bureau of Commercial Fisheries,
P. O. Box 3830,
Honolulu, Hawaii 96812

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Report of the Symposium on the Cooperative Study of the Kuroshio and Adjacent Regions (CSK)

Organized through the joint efforts of UNESCO,
FAO, and East-West Center
Honolulu, Hawaii, USA
29 April - 2 May 1968

REPORT AND ABSTRACTS OF PAPERS

Prepared by John C. Marr
as editor
in collaboration with the
Marine Biology and Environment Branch
Fishery Resources and Exploitation Division
FAO, ROME

and the

Office of Oceanography
UNESCO, PARIS

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, November 1968

EDITORIAL NOTE

This publication is part of the proceedings of the Symposium on the results of the Cooperative Study of the Kuroshio and Adjacent Regions (CSK) organised jointly by UNESCO and FAO with the support of the East-West Center, and held in Honolulu from 29 April to 2 May 1968 as a contribution to the cooperative study organised under the auspices of IOC. The present volume, issued by FAO, containing the general report and abstracts of papers presented at the Symposium was prepared and edited by John C. Marr, Area Director, Bureau of Commercial Fisheries, Honolulu, in collaboration with the Marine Biology and Environment Branch, Department of Fisheries, FAO, Rome and the Office of Oceanography, UNESCO, Paris. The full text of the contributed papers will be published in due course, together with an author index and subject index.

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GENERAL REPORT

1. INTRODUCTION

The Symposium was organized jointly by the Intergovernmental Oceanographic Commission of the United Nations Educational, Scientific and Cultural Organization (UNESCO), the Fishery Department, Food and Agriculture Organization of the United Nations (FAO), and the Office of Programs and Conferences, East-West Center of the University of Hawaii (EWC). It was held at the East-West Center, Honolulu, Hawaii, U.S.A. from 29 April to 2 May 1968. The contributions of the sponsoring organizations were:

UNESCO: Agreement with the EWC for holding the Symposium; travel expenses and subsistence of certain invited participants.

FAO: Travel expenses and subsistence of certain invited participants; publication of the volume containing the Report and the Abstracts of Papers.

EWC: Local arrangements including the provision of the meeting facility; travel expenses and subsistence of certain invited participants.

The Honolulu Laboratory, U.S. Bureau of Commercial Fisheries also assisted in making local arrangements and in providing document services.

2. BACKGROUND

The CSK was first proposed at the UNESCO Second Regional Meeting of Marine Sciences Experts in East and Southeast Asia held in Manila, 5-8 March 1962 and was recommended at the Intergovernmental Oceanographic Commission (IOC) Second Session held in Paris, 20-28 September 1962. Specific plans were developed at the UNESCO Meeting of Marine Sciences Experts on the Kuroshio Region held in Tokyo, 29-31 October 1963. The CSK was formally adopted at the IOC Third Session held in Paris, 10-19 June 1964. A CSK International Coordinating Group (ICG) was constituted, composed of National Coordinators and Assistant National Coordinators appointed by the participating countries. The ICG has met five times.

First Meeting	Manila	8-11 February 1965
Second Meeting	Paris	2 and 5 November 1965
Third Meeting	Tokyo	18-20 August 1966
Fourth Meeting	Bangkok	13-16 June 1967
Fifth Meeting	Honolulu	3-4 May 1968

An International Coordinator, Kiyoo Wadati, and an Assistant International Coordinator, John C. Marr, were chosen by the ICG at its First and Second Meetings, respectively. The countries initially participating in the CSK included China, Japan, Korea, Philippines, United Kingdom (Hong Kong), United States, U.S.S.R., and Viet Nam. They have subsequently been joined by Indonesia, Singapore, and Thailand.

The oceanographic aspects of the CSK include synoptic observations made in winter and summer, special studies in key areas, and observations made repetitively at selected reference stations. The fishery aspects of the CSK include studies of certain species selected on the basis of (1) the importance (weight, value, or both) of the fisheries based on them and (2) the fact that they are the basis of fisheries by two or more countries.

The Symposium, with John C. Marr as Convenor, was organized in five sections: The first was concerned with general reviews by countries, with Kiyoo Wadati as Chairman. The second was concerned with oceanography, with Kwan Ming Chan as Chairman. The third was concerned with plankton, with Tham Ah Kow as Chairman. The fourth was concerned with fishery, with Deb Menasveta as Chairman. The fifth and final section, with John C. Marr as Chairman, received the reports of the Chairmen of the sections on oceanography, plankton, and fishery.

3. REPORT OF OCEANOGRAPHY SECTION

A total of 21 papers on oceanography (physical oceanography and marine geology) was presented. Subject matters varied widely and some papers dealt with several topics; by category of topics the breakdown of the papers presented was:

Dynamics of the Kuroshio and related current	18
Distribution of oceanographic parameters	11
Bottom phenomena and marine geology	2

Out of 21 papers, 3 papers discussed the problem in general, while the majority of the papers, 18 in number, concentrated on description of specific material of the Pacific.

With regard to the origin of data, 14 papers were based upon the CSK data only and 5 upon non-CSK historical data, while 6 were on both.

Analysis of CSK data by several authors revealed the existence of an eastward movement of surface waters in the form, most likely, of a continuous belt between 20° and 25°N. A theoretical study of wind driven horizontal circulation had predicted the existence of such a current. It was suggested that this newly discovered current be called the "Subtropical Countercurrent." Details of the current were, however, not known at present. Therefore, it is considered that further elaborated studies were necessary, not only in the western Pacific but also in the other oceans.

The transport of the Kuroshio at various sections and the related currents such as the North Pacific Equatorial Current, the Mindanao Current, etc. were computed with the CSK data; the values were, however, not always compatible.

Comparing the Kuroshio with its homologue in the Atlantic Ocean, the Gulf Stream, the meandering of the Kuroshio south of Japan and existence of the Izu-Bonin Ridge were considered as characteristics of the Kuroshio. Detailed studies on the influence of the ridge on the southern route of the Kuroshio south of Japan might contribute effectively on the better understanding of the western boundary currents. Similarly, the possible importance of the Emperor Seamount Chain was noted. It was noted that within the area originally designated as the CSK area, some parts have not been covered by CSK cruises.

Therefore, the Symposium recommends the following investigations:

a. Investigation of the Subtropical Countercurrent.

b. Investigation of the Equatorial Current and the Kuroshio upstream of Japan (with emphasis on transport).

c. Investigation of the southern route of the Kuroshio and the influence of the Izu-Bonin Ridge and the Emperor Seamount Chain on the Kuroshio.

d. Investigation of the coastal and interisland shelf areas of the western Pacific and the South China Sea.

e. Investigation of the area south of 20°N in the CSK area.

The needs of coordinated efforts to study air-sea interaction and also inclusion of atmospheric studies in the CSK program were recognized. For this purpose the Symposium recommends the investigation of ocean-atmosphere interaction.

With regard to the methods and techniques for future studies, the conventional oceanographical observations for the Kuroshio would not afford any remarkable progress on the understandings of the Kuroshio. Fruitful results might be obtained using newly developed instruments. It was also noted that synoptic and synchronous observations undertaken as CSK projects had contributed greatly to the understanding of the Kuroshio and adjacent regions, but in some areas no such observations have been carried out. In order to carry out observations with modern techniques and concepts, it is quite important to fix ship positions accurately, but adequate navigational aids are at present not available in the whole region, particularly in the southern part of the CSK area.

The Symposium recommends the following:

a. Undertake additional synoptic and synchronous observations in holiday areas, especially in the subtropical western Pacific.

b. Encourage use of new techniques such as STD, expendable BT, Swallow floats, and other methods of direct current measurement, methods of chemical analysis both improved and automatic, and airborne radiation thermometer.

c. Encourage improvements in navigational aids, including recommendation to make satellite navigation internationally available.

The compatibility of data obtained by an international cooperative study was considered essential. To achieve this goal, the Symposium recommends:

a. Undertake comparisons of methods of analysis.

b. Study the most effective way of quality control of data.

The importance of biological studies of the ocean should not be overlooked. In this connection the Symposium recommends that the study of biological effects such as nutrient cycles and primary productivity be emphasized.

It was the consensus that another symposium on CSK will be very desirable. For the success of such a symposium it might be desirable to consider recommending reports be presented on specific subjects in order to encourage study of these subjects, especially the comparison of methods and CSK reference stations. The representative of the Pacific Science Association, Dr. Miyake, Chairman of the Standing Committee on Marine Science, extended an invitation to hold a symposium at the forthcoming Pacific Science Congress in Australia in 1971.

The Symposium suggests that consideration be given to making a distinction between problems requiring international cooperation and other problems of more nearly national interest. Another distinction is between time dependent and nontime dependent phenomena.

4. REPORT OF PLANKTON SECTION

A total of 15 papers was read at the Symposium. They can be classified into the following categories:

Taxonomic papers
Distribution and environmental papers
Miscellaneous papers

4.1 Taxonomic Papers

Under this category there were two papers, viz: one on the euphausiids of Korean waters by Hong and one on ostracods from Taiwan Straits by Tseng.

4.2 Distribution and Environmental Papers

a. Regional distribution of major systematic groups of zoöplankton in Kuroshio region collected by Japanese ships 1965-66 by Yamazi.

b. Marine biology investigations of Kuroshio region by Kun.

c. Effect of environmental factors on macro-zooplankton around Taiwan by Yu and Lee.

d. Plankton in Singapore waters in relation to environment by Tham, Khoo, and Chua.

e. Zooplankton distribution and abundance in Lamon Bay (Philippines) by Magnusson, Tan, and Rizalina.

f. Chaetognaths in Korean waters by Park.

g. Chaetognaths around Taiwan by Liaw.

h. Copepods around Taiwan by Tan.

4.3 Miscellaneous Papers

a. Particulate organic matter in seas off Japan by Saijo.

b. Primary production in Kuroshio area by Saijo.

c. Plankton settling volumes around Taiwan 1965 by Tseng.

d. Biological structures in sea south of Japan by Motoda, Kawamura, and Ishii.

e. Preliminary report on zooplankton processing in Japanese CSK studies by Motoda, Irie, and Yamazi.

These papers form a useful contribution to the knowledge on plankton in the region and the data presented were discussed at some length by those present, although it was felt that more planktologists, especially those who presented papers, should have been present.

It is significant that the majority of the papers dealt with the distribution of plankton organisms in relation to the environment.

It was generally felt that the plankton data collected would be more meaningful if they could be presented in a form similar to that given in Yamazi's paper.

The Plankton Group submits the following recommendations for consideration:

a. In order to get a clearer picture of distribution of planktonic organisms in space and time, future work should be centered around the interrelationships between the planktonic organisms and the environment.

b. A second CSK symposium would be most useful but in organizing for such a symposium, steps should be taken to ensure that sufficient planktologists, in particular those who are presenting papers, would be present to make discussion fruitful. In such a second symposium, it is proposed that taxonomic papers will be mentioned by title only unless the author is present.

c. In order that the plankton data collected would be more meaningful, it is recommended that the International Coordinator for CSK should find ways and means to publish the data in a form similar to that given in Yamazi's paper.

5. REPORT OF FISHERY SECTION

A total of 29 fishery papers was presented during the 2-day Symposium. Subject matter varied widely and each of the eight species or group of species selected for intensive study by CSK participants was represented by at least one paper. By category the breakdown of the papers presented was:

Fishery-oceanography	3	Scomberomorus spp.	1
Biological (general)	3	Rastrelliger spp.	3
Bottom trawl (general)	4	Pseudosciaena manchurica	1
Stolephorus spp.	3	Saurida spp.	2
Cololabis saira	1	Nemipterus spp.	3
Katsuwonus pelamis	4	Others	1

General emphasis of the Symposium was on bottom trawl fishing, principally because of the importance of this type of fishing in the western Pacific, especially in Southeast Asia. Also, several of the bottom dwelling fish species usually taken by bottom trawl gear are included in the list of selected species. These are Saurida spp., Nemipterus spp., and Pseudosciaena manchurica.

5.1 Taxonomy

It became evident in the early stages of the CSK program that difficulty would be encountered in the identification of certain groups of fishes. The Coordination Group of the CSK program in response to these problems has already requested Mr. T. Matsui of the Scripps Institution of Oceanography, University of California, to act as a referee for Rastrelliger spp., Mr. W. Chan of Hong Kong Agriculture and Fisheries Department as referee for Scomberomorus spp., and Mr. I. Ronquillo, Department of Agriculture and Natural Resources, Philippine Fisheries Commission, as referee for Stolephorus spp. in collaboration with Dr. Tham Ah Kow of the University of Singapore.

The participants of the Fishery Section of the Symposium (referred to hereafter as the Group) felt, however, that Nemipterus spp. and Saurida spp. also needed clarification and recommends selection of referees for these two groups. The Group recommended that the Assistant International Coordinator for Fisheries approach Dr. S. Shindo of Seikai Regional Fisheries Research Laboratory to act as a referee for Saurida spp. and Dr. D. Eggleston of the Hong Kong Agriculture and Fisheries Department as referee for Nemipterus spp.; the latter to work in close collaboration with Dr. G. Kühlmorgen-Hille of the Marine Fisheries Laboratory, Bangkok, Thailand, and Dr. F. Talbot of the Australian Museum.

In resolving taxonomic problems, the referees will need access to specimens from various areas. In this connection there are two possible approaches. The first is for participating countries to collect and ship specimens to referees for identification. Another is to obtain funds to provide for travel and other expenses to permit referees to visit the various countries in order to collect the needed specimens. The Group felt that both approaches should be pursued.

The following specific recommendations made by the Group on taxonomic problems are:

a. Request Mr. I. Ronquillo to advise the Coordination Group of the basis on which he decided to consider Stolephorus pseudoheterolobus as a synonym of S. heterolobus.

b. Determine the distribution of Rastrelliger faughni.

c. Encourage countries to provide specimens of commercially important species to Mr. W. Chan of the Hong Kong Agriculture and Fisheries Department, in order that he may complete the fish cards requested by the Indo-Pacific Fisheries Council.

d. Add Decapterus spp. and the family Sciaenidae to the existing selected list of CSK species.

5.2 Stock Identification

The Group was of the opinion that stock identification is essential in studies leading to the rational exploitation of fishery resources. It therefore recommends identification of the stocks of the various selected species be made by participating countries which exploit these species. This identification could be accomplished by the study of subpopulations using serological and immunogenetic methods and by tagging, accompanied by analyses of catch and effort data and the distribution of eggs and juvenile fish.

The following specific recommendations made by the Group on stock identification problems are:

a. Clarify the population structure of Rastrelliger brachysoma in the Gulf of Thailand and adjacent waters.

b. Clarify the population structure of Cololabis saira in the Sea of Japan and the western North Pacific. The methods of tagging and subpopulation studies by serological and immunogenetic techniques should be continued and encouraged for this species.

c. Continue the study of the relationship of skipjack tuna in the southwest Pacific Ocean and other areas of the Pacific by means of tagging and serological and immunogenetic techniques.

5.3 Stock Assessment

The Group agreed that in the evaluation leading to the rational exploitation of fishery resources, participating countries should examine carefully the catch and effort data already collected and that, if these data have not yet been compiled, the collection of proper catch and effort data should be initiated without delay.

The following specific recommendations made by the Group on stock assessment problems are:

a. Conduct stock assessment studies of the more important species taken by the trawl fisheries in the CSK area.

b. Continue studies of age and growth of Rastrelliger brachysoma by the method of size-frequency analyses. This study should be accompanied by an experimentally-designed tagging program to collect independent age and growth data, for comparative purposes.

c. Participating countries should be encouraged to commence stock assessment studies of the commercially important species. Exchange of data and other pertinent information among CSK participants should be encouraged, particularly through the FAO Fishery Data Center as agreed upon by the CSK International Coordination Group at the Third Meeting.

5.4 Exploratory Fishing Survey

With respect to ground fish resources of the Sunda Shelf, the Group agreed that due to the lack of sufficient data from previous trawling surveys in the central part of the Sunda Shelf, in the waters around Anambas and Natuna Islands and in the waters off North Borneo and Sarawak coasts, trawling surveys through the mutual effort of participating countries in the region should be repeated in these waters. Consideration should be made of time and space factors in order to obtain sufficient data to reach definite conclusions as to the status of the demersal resources in these waters. The Group also recommends the initiation of trawl fishing surveys in the Java Sea.

In connection with the trawl fishing surveys in the South China Sea, the Group recommended that plankton and other environmental studies be carried out.

As for the study of the skipjack resources in the western Pacific, the Group recommends exploratory fishing using various types of fishing gear be initiated.

As for the study of the saury resources, the Group recommends conducting exploratory fishing using stick-held net with night lamp and gill nets in the western and central Pacific of the CSK area.

5.5 Intercalibration of the Fishing Gear

The Group repeated the recommendation made at the Fourth Meeting of the Coordination Group in Bangkok in 1967; that, when possible, an intercalibration of trawlers and trawl gear be made in order to arrive at conversion factors which can be used in the development of standardized catch rates.

The Group recommended that this intercalibration should initially involve research trawlers of participating countries, and could most suitably be conducted in connection with the exploratory fishing survey programmed for the South China Sea.

5.6 Environmental Studies

Several papers contributed by Japan and Korea have demonstrated the effects of currents, eddies, oceanic fronts, etc. of the Kuroshio and associated currents on the transport of fish eggs and larvae of saury, mackerel, hairtail, etc. and on the fluctuation of the stock sizes of these fish. The Group was of the opinion that this type of study should be continued and invited participating countries to initiate such a program of study, when possible.

In order to prevent marine pollution (including oil pollution) and to improve the marine environment, mixing, diffusion and transport through the Kuroshio and other associated current systems should be carefully studied.

In future studies, tagging should be used to supplement the knowledge of the movement of certain stocks of fish along and within the Kuroshio Current.

5.7 Mariculture

The Group was of the opinion that participating countries interested in the culture of marine fishes, including tunas, should be encouraged to carry out these studies.

5.8 Publication of Naga Expedition Reports

The Group was informed that between October 1959 and December 1960, Thailand, Viet Nam, and the United States of America carried out an oceanographic expedition (Naga Expedition) which included fisheries resources surveys in the Gulf of Thailand and the South China Sea.

Results of this expedition have been published in part in a restricted form, e.g., handbooks or circular reports. These reports have been sent to selected institutions and are not available for general distribution. Considering the general lack of information of the biota and environment of the South China Sea and recognizing the great contribution the publication of the Naga Expedition could give towards the planning of future surveys of the South China Sea, the Group strongly recommends effort be made to publish the results of the Naga Expedition.

5.9 Intensification of the CSK Program in the South China Sea

The Group recommends strongly that the survey of the CSK program in the South China Sea be intensified.

6. RECOMMENDATIONS

The recommendations arising from the CSK Symposium were presented to the ICG/CSK Fifth Meeting. The final set of recommendations adopted at the Fifth Meeting includes those from the Symposium as well as some arising during the course of the Fifth Meeting, as follows:

6.1 Bathymetric Studies

No. 1 The International Coordination Group for CSK requests the International Coordinator to maintain close contact with the Hydrographic Department of the Maritime Safety Agency, Japan to obtain information on specific areas and/or tracks to which sounding data are desired, and requests further such information be publicized by the CSK Newsletter.

The Group recommends that CSK participating Member States pay due consideration to traversing such areas during appropriate CSK cruises as far as possible.

6.2 Standard Oceanographic Equipment

No. 2 With reference to Resolution V-21 of the Fifth Meeting of IOC, the Group recommends that UNESCO assist in the provision of standard oceanographic equipment (e.g., salinometer, plankton net, bathythermographs, etc.).

6.3 Oceanography

No. 3 The Group recommends the following investigations:

a. Investigation of the Subtropical Countercurrent.

b. Investigation of the Equatorial Current and the Kuroshio upstream of Japan (with emphasis on transport).

c. Investigation of the southern route of the Kuroshio and influence of the Izu-Bonin Ridge and the Emperor Seamount Chain on the Kuroshio.

d. Investigation of the coastal and interisland shelf areas of the western Pacific and South China Sea.

e. Investigation of the area south of 20°N in the CSK area.

No. 4 The needs of coordinated efforts to study air-sea interaction and also inclusion of atmospheric studies in the CSK program were recognized. For this purpose, the Group recommends the investigation of ocean-atmosphere interactions.

No. 5 With regard to methods and techniques of future studies, the Group recommends:

a. Undertake additional synoptic and synchronous observations in holiday areas, especially in the subtropical western Pacific.

b. Encourage use of new techniques such as STD, expendable BT, Swallow floats, and other methods of direct current measurement, methods of chemical analysis both improved and automatic, and airborne radiation thermometer.

c. Encourage improvements in navigational aids, including recommendation to mak satellite navigation internationally available.

No. 6 The compatibility of data obtained by an international cooperative study was considered essential. To achieve this goal, the Group recommends:

a. Undertake comparisons of methods of analysis.

b. Study the most effective way of quality control of data.

No. 7 The importance of biological studies of the ocean should not be overlooked. In this connection the Group recommends that the study of biological effects such as nutrient cycles and primary productivity be emphasized.

6.4 Plankton

No. 8 In order to get a clearer picture of distribution of planktonic organisms in space and time, the Group recommends future work should be centered around the interrelationships between the planktonic organisms and the environment.

No. 9 A second CSK symposium would be most useful but in organizing for such a symposium, the Group recommends steps should be taken to ensure that sufficient planktologists, in particular those who are presenting papers, would be present to make discussion fruitful. In such a second symposium, it is proposed that taxonomic papers will be mentioned by title only unless the author is present.

No. 10 In order that the plankton data collected would be more meaningful, the Group recommends that the International Coordinator for CSK should find ways and means to publish the data in a form similar to that given in Yamazi's paper.

6.5 Fisheries

No. 11 Concerning taxonomic problems, the Group recommends:

a. Request Mr. I. Ronquillo to advise the Coordination Group of the basis on which he decided to consider *Stolephorus pseudoheterolobus* as a synonym of *S. heterolobus*.

b. Determine the distribution of *Rastrelliger faughni*.

c. Encourage countries to provide specimens of commercially important species to Mr. W. Chan of Hong Kong, in order that he may complete the fish cards requested by the Indo-Pacific Fisheries Council.

d. Add *Decapterus* spp. and the family Sciaenidae to the existing selected list of CSK species.

No. 12 Concerning stock identification problems, the Group recommends:

a. Clarify the population structure of *Rastrelliger brachysoma* in the Gulf of Thailand and adjacent waters.

b. Clarify the population structure of *Cololabis saira* in the Sea of Japan and the western North Pacific. The methods of tagging and subpopulation studies by serological and immunogenetic techniques should be continued and encouraged for this species.

c. Continue the study of the relationship of skipjack tuna in the western Pacific Ocean and other areas of the Pacific by means of tagging and serological and immunogenetic techniques.

No. 13 Concerning stock assessment problems, the Group recommends:

a. Conduct stock assessment studies of the more important species taken by the trawl fisheries in the CSK area.

b. Continue studies of age and growth of Rastrelliger brachysoma by the method of size-frequency analyses. This study should be accompanied by an experimentally-designed tagging program to collect independent age and growth data for comparative purposes.

c. Participating countries should be encouraged to commence stock assessment studies of the commercially important species. Exchange of data and other pertinent information among CSK participants should be encouraged, particularly through the FAO Fishery Data Center as agreed upon by the CSK International Coordination Group at the Third Meeting.

No. 14 With respect to ground fish resources of the Sunda Shelf, the Group recommends that due to lack of sufficient data from previous trawling surveys in the central part of the Sunda Shelf, in the waters around Anambas and Natuna Islands and in the waters off North Borneo and Sarawak coasts, trawling surveys through the mutual effort of participating countries in the region should be repeated in these waters. Consideration should be made of time and space factors in order to obtain sufficient data to reach definite conclusions as to the status of the demersal resources in these waters. The Group also recommends the initiation of trawl surveys in the Java Sea. In connection with the trawl fishing surveys in the South China Sea, the Group recommends that plankton and other environmental studies be carried out.

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No. 16 As for the study of the saury resources, the Group recommends conducting exploratory fishing using stick-held net with night lamp and gill nets in the western and central Pacific of the CSK area.

No. 17 The Group repeats the recommendation made at the Fourth Meeting of the Coordination Group in Bangkok in 1967; that, when possible, an intercalibration of trawlers and trawl gear be made in order to arrive at conversion factors which can be used in the development of standardized catch rates.

The Group recommends that this intercalibration should initially involve research trawlers of participating countries, and could most suitably be conducted in connection with the exploratory fishing survey programmed for the South China Sea.

No. 18 The Group was informed that between October 1959 and December 1960, Thailand, Viet Nam, and the United States of America carried out an oceanographic expedition (Naga Expedition) which included fisheries resources surveys in the Gulf of Thailand and the South China Sea. Results of this expedition have been published in part in a restricted form, e.g., handbooks or circular reports. These reports have been sent to selected institutions and are not available for general distribution. Considering the general lack of information of the biota and environment of the South China Sea and recognizing the great contribution the publication of the Naga Expedition could give towards the planning of future surveys of the South China Sea, the Group strongly recommends effort be made to publish the results of the Naga Expedition.

6.6 South China Sea Program

No. 19 The Group recommends strongly that the survey of the CSK program in the South China Sea be intensified.

6.7 Publication of Results of CSK Symposium

No. 20 With regard to the publication of the results of CSK Symposium, the Group recommends:

a. There be two publications arising from the CSK Symposium:

(1) The Report which would include (1) a Summary Report covering the highlights of scientific results and the recommendations, and (2) the abstracts of the submitted papers.

(2) The Proceedings which would include the submitted papers.

b. The Report be published in the immediate future by FAO and UNESCO.

c. The Proceedings be published as soon as possible, perhaps by the East-West Center Press if this can be arranged.

d. All submitted papers be accepted for publication except those which have already been published elsewhere in English and those which do not meet the generally accepted standards for scientific papers.

e. The Convenor of the Symposium, John C. Marr, be asked to serve as editor of the Report and the Proceedings.

6.8 Regional Equipment Pool

No. 21 With reference to recommendation No. 3 of the Fourth Meeting of Marine Science Experts in Southeast Asia, the Group recommends that UNESCO initiate the setting up of a Regional Equipment Pool for the promotion of more efficient distribution and maintenance of equipment.

6.9 Synoptic Surveys

No. 22 The Group recognized the importance and the necessity of continuing the CSK at this stage. The Group agreed to terminate the cooperative synoptic surveys in the Pacific area after the summer cruises in 1970. The emphasis then should be put on synoptic surveys in subtropical and tropical areas in the western Pacific, where observations were rather scarce, and on stations occupied for long periods at selected points of the region.

The situation with regard to cooperative synoptic surveys in the South China Sea is different from that in the Pacific area, since the former began later than the latter.

At the present moment, it would appear that the cooperative synoptic surveys in the South China Sea and adjacent waters will extend beyond summer 1970. The Group recommends that the International Coordinator in cooperation with Dr. Deb Menasveta be requested to coordinate with the countries concerned in this survey to produce a basic plan and timetable for this survey and to circulate to National Coordinators not later than 3 months in advance of the next ICG/CSK meeting.

The Group recommends that another symposium be held in the first half of 1970 in order to review the scientific achievements of CSK and to advise ICG/CSK on the future of CSK.

6.10 Joint IPFC-CSK Meeting

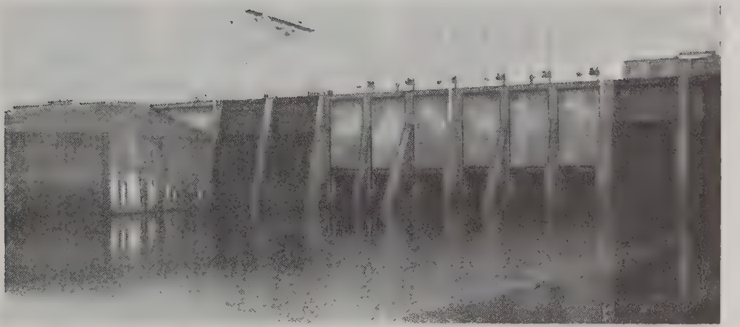
No. 23 Noting that the 13th Session of the Indo-Pacific Fisheries Council will be in Australia in October 1968, the Group recommends that a joint IPFC-CSK meeting be made a part of that session.

6.11 KDC Atlases

No. 24 The Group recommends that before the KDC Atlases are bound, unbound copies be circulated to ICG/CSK. When approvals have been received from the National Coordinators, the cover will be added, without the word "Provisional," i.e., this will be the final form of the Atlas.

Sections of the report not reprinted here are:

7. List of participants (p. 12-15).
8. Author index and titles of papers (p. 16-20).
9. Abstracts of papers (p. 21-57).



French Creek Pumping Station at Snohomish was the site of the fish survival study.

Fish survive pumping plant

Cooperative study shows 80 percent of young salmon make trip without injury

By L. Dean Marriage and Richard N. Duncan
Regional fisheries biologist, SCS, Portland, Oreg., and fishery research biologist, U. S. Bureau of Commercial Fisheries, Pasco, Wash.

Juvenile salmon survived a fast, rough trip through a large flood pump in a cooperative test conducted by the Soil Conservation Service and the Bureau of Commercial Fisheries at Snohomish, Wash.

Objectives of the study were to determine whether young fish can survive the extensive pumping of floodwaters that is a necessary part of land and water management in the coastal plains of the Pacific Northwest and to explore the causes of fish deaths observed.

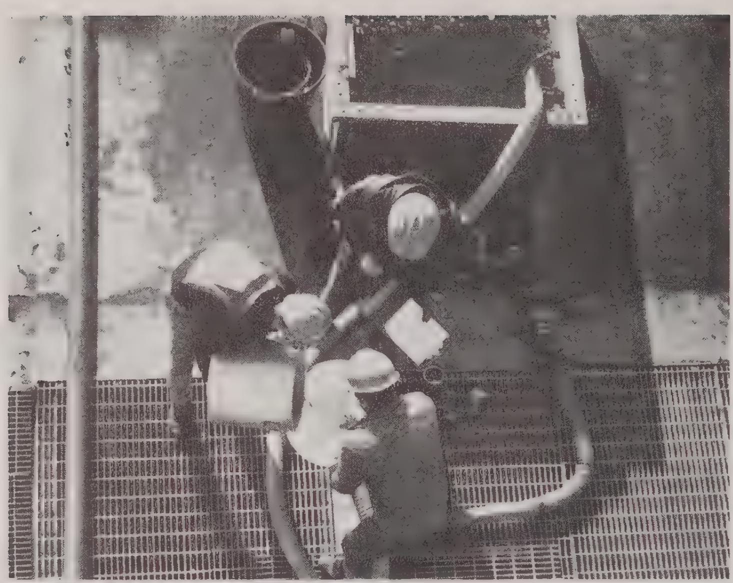
The study was carried on for 3 weeks in the spring of 1967 at the French Creek Pumping Station, part of the French Creek Watershed Project.

The Bureau of Commercial Fisheries provided funds, experienced help, and time-tested fish handling equipment; Bureau of Sport Fisheries and Wildlife provided juvenile salmon; Soil Conservation Service provided funds, facilities, help, and coordination services; Washington Department of Fisheries provided coho salmon fingerlings and use of hatchery facilities; Washington Department of Game provided trout; and the French Creek Flood Control District provided the use of its pumping plant.

The pump used in the test has a 3-bladed propeller 41 inches in diameter turning at a fixed rate of 440 r.p.m. and delivering about 70,000 g.p.m. at a lift of 9 feet—the average lift during the study. A large steel flap gate was attached to the discharge outlet.

Tattooed fingerlings were picked up at the Washington Department of Fisheries Skykomish Salmon Hatchery at Sultan and transported by truck in specially designed holding pens and live tank to the French Creek pumping plant, about 20 miles away. Each lot consisted of 100 coho salmon fingerlings averaging 4¼ inches long. The fish were tattooed near the head and tail with an identifying pigment.

At the pumping plant, the fish were transferred to plastic buckets and transported to the pump. They were washed into the pump by



Three men, seen from above, pour water and fish ino one of three hoses leading to different levels at the pump intake 40 feet below the deck. Funnel is shown at left on one of the hoses. The fish were recovered in a 45-foot long collection net and floating trap (right) attached to the discharge outlet of the pump.

means of 3-inch diameter flexible hose leading from the deck about 40 feet to one of three positions at the intake of the pump.

The fish passed through the pump system to a point below the outlet where they were recaptured in a 45-foot long tapered nylon net and trap attached to the discharge outlet.

The only times the fish were removed from the water were in the tattooing process and in removing them from the trap. All other transfers were made in water without manual handling.

Back at the hatchery, the live and dead fish were separated, identified by the color of the tattoo mark, and counted. The dead were then examined to determine the cause of death. The live fish were placed in holding pens in a hatchery pond for observation of delayed mortality.

The following results were observed:

(1) Eighty percent of the coho fingerlings passing through the pump survived without injury.

(2) Position of entry of the fish into the pump's intake did not affect the rate of survival.

(3) The flap gate which causes extreme water turbulence was not a factor in fish injuries.

(4) Results of limited tests on different sizes of fish (1¾ to 9 inches long) showed smaller fish survive better than larger ones.

(5) Introducing compressed air into the pump at a fixed rate did not alter the survival rate of fish tested.

(6) Most fish injuries were of a mechanical type that could be caused by the fish coming into contact with the propeller, guide vanes, or diffuser vanes within the pump.

The interagency pooling of experience, finances, equipment, manpower, and fish resources reduced the cost of the study to a fraction of what it would have been for a single agency. The information will be helpful in understanding the effects of pumps on fish and in planning future pump installations for the safety of fish. ◆

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The Use of Glass Wool Plugs during Kjeldahl Nitrogen Analyses

When organic nitrogen is determined by the Kjeldahl procedure, precautions must be taken to prevent sulfuric acid fumes from contaminating the laboratory. Usually an exhaust fan is used for this purpose; either the necks of the boiling flasks are placed in an exhaust manifold or the analysis is conducted in a ventilated hood. Another procedure consists of plugging the necks of the boiling flasks with commercially available tubes made of a porous ceramic substance. If the tubes do not fit tightly, however, they may be blown from the flask.

We have discontinued use of ceramic tubes, in favor of plugs of a borosilicate glass wool. This material conforms exactly to boiling flask necks of any size, either tooled or untooled, and effectively prevents the escape of sulfuric acid fumes. We have used the plugs in many thousands of analyses and have yet to experience a blow-out. The number of analyses that can be made at one time is not limited by available manifold or hood space, but only by laboratory working space.

Bureau of Commercial Fisheries
Biological Laboratory
Galveston, Texas 77550

K. T. Marvin and R. R. Proctor, Jr.

PAUL M. MAUGHAN:

SPACECRAFT FOR FISHERY RESEARCH

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1 INTRODUCTION

Man's recently acquired ability to put instrument-carrying spacecraft into orbit around the earth suddenly provides a new and potentially powerful tool with which to examine our planet. Because most spacecraft spend three quarters of their orbiting time over the oceans which contain innumerable fish, it is only natural that we look to fishery research as one possible application of spacecraft technology.

Spacecraft have two unique research capabilities: synoptic coverage and repeatibility. Only with a spacecraft can we achieve a truly synoptic coverage of the ocean. The spacecraft can, when placed in a polar orbit, cover all parts of the ocean with ease without regard to weather, fuel limitations, navigational difficulties, and other hazards of surface-bound methods. Moreover, in order to study the relationship between events occurring in the ocean at one time with those occurring at a later time, the same area must be covered over and over again. Spacecraft are particularly adaptable to this type of repetitious coverage.

It is important to understand that in the initial stages of using spacecraft for fishery research, they can provide only complementary information to that collected from more conventional platforms. Thus, we cannot expect that spacecraft will eliminate the need for ships and buoys -- this can only partially fill information gaps presently so evident in surface-collected data.

The use of spacecraft in no way implies that it is the utopia of data collection systems. Whereas we may expect to identify from spacecraft ocean phenomena related to abundant fish stocks, there may be alternate and less costly means of identifying the

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same phenomena. Thus, spacecraft should not necessarily be used to collect data when equally reliable data can be collected by other more cost-effective methods.

Spacecraft can provide only that data which is available through "remote sensing", that is, the measurement of some property of a phenomenon without having the measuring device physically in contact with it. Temperature is an example of one property which can be remotely sensed. To date, however, there has been no definitive measurements of marine biological activity from space. Nonetheless, the remote detection from aircraft of near-surface schools of fish has shown that all craft (both air- and space-) may be useful for fishery research.

2 REMOTE SENSORS

There are at least two ways that remote sensor data can be effectively used: in identifying a phenomenon or in determining something about its properties. An example of an identifiable phenomenon is upwelling with the surface temperature structure of the upwelled area as an important property. Identification can best be made on the basis of size, shape, or some other criterion with a remote sensor that duplicates our visual senses such as the duplication of our visual senses by photography. Properties such as composition can best be determined on the basis of electromagnetic absorption characteristics with a remote sensor such as a spectrometer.

Because most remote sensing in fishery research is concerned with the identification aspect, sensor systems presently considered to be of prime importance include:

4,000 to 7,000	angstrom wavelength sensors (visible)
1 to 100	micron wavelength sensors (infrared)
1 to 10	centimeter wavelength sensors (microwave)

To provide background related to fishery research associated with each of the prime sensors listed above, a discussion of each sensor follows.

2.1 Visible wavelength sensors

There are two major methods of recording light in the visible wavelengths: color and multispectral photography. Color photographs are generated by exposing a monopack color film to the incoming light. A multispectral photograph is generated by color separation negatives taken with red, green, and blue filters, in bands of the spectrum where the usual primary color differences peak. The records obtained can be recombined during printing and viewing to produce color prints and transparencies which are superior in resolution and color saturation to those taken by monopack color films.

The advantage of color by multispectral photography is that, unlike a color film, where all the exposure values of highlights and shadows are fixed, each multispectral separation negative may be controlled separately in filtering, exposure, processing, and in enhancing and printing. The scientist can examine each record separately, or in combination with others. All grades of color derivations and masking operations can be obtained directly.

The resolution of a photographic sensor system is dependent on the focal length and resolving power of the lens system and the quality of the film. Objects less than a meter in diameter are generally resolvable with currently available aerial photographic systems and approximately one hundred meters in diameter with spacecraft photographic systems such as were used by the astronauts. A newly designed multispectral imaging system proposed for the Earth Resources Observation Satellite (EROS) is theoretically able to resolve objects approximately 30 meters in diameter.

2.2 Infrared wavelength sensors

The infrared (IR) sensors will detect electromagnetic radiation in the wavelength regions between 1 and 100 microns. There are three major types of IR sensors: imagers, radiometers, and spectrometers.

The infrared imaging sensor produces pictorial data in which shapes are utilized to detect and identify phenomenon such as water mass boundaries. The radiometer measures the absolute energy emitted and/or reflected from objects and thereby determines size and location. The spectrometer is used to detect phenomenon or constituents of the environment such as water vapor and temperature gradients below the sea surface.

The imaging system is similar to an ordinary camera system except that there exists no image-reproducing device such as a film or television. Infrared experiments have been mainly conducted in the 3 to 5 micron atmospheric transmission "window" (a wavelength interval). More recently, sensors capable of operating in the 7 to 13 micron window have been flown in aircraft. The longer wavelengths give higher sensitivity because they better match the thermal emission wavelengths from the water.

Resolution in the order of 30 meters and 0.3 C^{o} can be obtained with a high quality IR sensor system. Resolutions in an order of magnitude greater are commonplace with more conventional equipment.

2.3 Microwave wavelength sensors

The inherent day-night all-weather capability of the microwave sensor system offers certain advantages over the multispectral and infrared sensor systems. A microwave sensor is used primarily as a passive device and detects the energy emitted by all phenomena having temperatures greater than absolute zero. The emissivity and reflectivity of the surface under observation is of prime importance and is altered variously by the changing condition of the sea surface.

A microwave radiometer usually consists of a directive antenna feeding a wideband receiver with provisions for switching the receiver input from the antenna to a calibrated source of known temperature. The electronic equipment can be mainly solid state with attendant high reliability, low power consumption, and small size.

The resolving capabilities of a microwave sensor are generally less than those of the infrared sensor. Resolutions between 300 and 10,000 meters for the imager and between 3 and 10,000 meters for the radiometer with temperature resolution 0.3 to 1.0 C^{o} are values commonly quoted for systems currently under development.

3 APPLICATION OF REMOTE SENSORS TO FISHERY RESEARCH

The application of remote sensors to the broad field of earth resources has been extensively documented. Included in almost all application discussions is the concept of spacecraft for fishery research. This has been manifested in the proposed utilization of remote sensor data for

- directly detecting large near-surface schools of fish, and
- observing and recording environmental phenomena that are related to the abundance and distribution of fish stocks.

This dual approach to the utilization of remote sensor data appears useful when we consider that it is necessary to provide a direct assessment of the fish stocks before any useful information can be derived from the indirect observation of those phenomena associated with productive fish areas.

3.1 Direct detection of fish stocks

A valuable segment of the total marine biological resources is composed of the surface-schooling pelagic fishes, including the herrings and tunas. Both industry and research organizations are currently making use of aircraft for schoolfish location and assessment, both directly and through photo reconnaissance techniques. Still, only limited areas have been surveyed in this manner resulting in difficulty in providing meaningful estimates of a far-ranging resource complement.

The use of remote sensors for the direct detection and assessment of fish stocks has not progressed beyond aerial observations from relatively low-flying aircraft. However, considerable information has been derived from the large number of color photographs currently available of surface-schooling fish.

The work of the Exploratory Fishing and Gear Research Base at Pascagoula, Mississippi, has provided a focal point for the study of fish detection by direct observations. The objective of this work is to study a method of fish stock assessment which will enable a regular timely dissemination of information to commercial fishermen on the availability of particular fish stocks.

Oblique photographs of wide areas of surface-fish school activity have been made (fig 1). A close scrutiny of these photographs reveal that although they show the broad areas the schools cover and various configurations the schooling fish assume (figs 2,3) they do not permit the evaluation of the schools as to tonnage or species.

In order to gain sufficient information with which to analyze photos of fish schools, two concurrent projects are being established. The first will involve a coordinated effort between the aircraft and commercial fishing vessels on which staff members will be stationed. Radio communication between the two units will provide information as to species of fish and quantities captured aboard the vessel. The second project will involve stationing a SONAR-equipped research vessel at the scene of the fishing operations. The SONAR will scan the underwater configuration of the fish schools giving depth and horizontal extent which can then be related to the photographs.

The extraction of the maximum information from each photograph is of primary importance. Multispectral analysis, referred to as "false color separation", has been developed by Ross of Philco-Ford Corporation (fig 4). This is accomplished by photographing a color transparency with 25 millimicron bandpass interference filters to produce a series of five negatives. This technique serves to increase the contrast of small color differences between the successive spectral bands. Color separations have revealed information not detectable on the original record.

The usefulness of the color separation technique has not been fully investigated but it is anticipated that it will aid in the interpretation of photographic records presently available and will enable the evaluation of this technique as a possible standard method of analysis of future photographic data.

Another method of photographic interpretation, densitometry, has the capability of measuring and recording minute differences in the thickness of film emulsion thereby depicting details which could not otherwise be observed. This may allow the photographic interpreter to determine the varying densities of fish within a school (fig 5).

Although it may be stretching the concept of the direct detection of fish to include the technique of fish oil identification by spectroscopy, it is known that surface-schooling pelagic fish in general exude oils which appear as surface slicks (fig 6). A recent laboratory study by Barringer Research Ltd. of the ultraviolet wavelength optical properties of various fish oils has produced some interesting results.

The basis for the experimental work was theoretically investigated by computing the polarization reflection effects of the air-oil-water interface with the effects of absorption in the oil taken into account. It was found that fish oils being agitated with the water form small lenses on the surface. This is radically different from the mineral oils which tend to form a monolayer under all conditions (fig 7). Results of the investigation showed that fish oils can be readily classified by a multiband photometric system based on the absorption spectra when the oil sample is viewed in transmission. However, in reflection, the oils are not readily detected or classified in the ultraviolet region of the spectrum. Preliminary work in the infrared region of the spectrum shows considerable promise for positive results.

3.2 Indirect detection of fish stocks

If oceanographic phenomena which are indicative of high productivity were identifiable with remote sensors, the search time for productive fishing grounds could be decreased. Forecasting productive fishing grounds would then depend largely on the ability of marine scientists to derive meaningful relationships betwen environmental conditions and the abundance and distribution of fish stocks.

For example, information as to the location of favorable temperature regimes (fig 8) is useful information to the fishermen. Also, the accurate and timely location of significant current systems (fig 9) and water mass boundaries (fig 10) could provide information which may be necessary before global fish forecasts are available.

An oceanographic analysis by Stevenson of the Bureau of Commercial Fisheries of photographs taken during the GEMINI flight series provides an excellent illustration as to the potential of space photography for the indirect detection of fish stocks. It must be noted, however, that the camera used during the GEMINI flight was a hand-held instrument which has provided imagery of a scale previously unfamiliar to the interpreter.

The Gulf of Mexico adjacent to southeast Texas and southwest Louisiana is shown in a GEMINI XII photograph (fig 11) taken by astronauts Lovell and Aldrin. An analysis of the photograph shows that longshore currents were flowing southwest partially in response to the brisk winds blowing from the northeast (see smoke plume at lower edge of photograph).

The lighter coloring off the coast is sediment-ladened waters moved out into the Gulf during the period of strong northerly winds. The light streak extending from the mouth of Galveston Bay is highly turbid water resulting from shelldredging operations within the lower bay.

The importance of being able to photograph the coastal waters of Texas and Louisiana is manifest in the very important shrimp fishery contained within this area. Two key events in the lives of these shrimp are their migration, as post-larvae into the coastal estuaries and as adults out of these estuaries. Detailed knowledge of coastal currents may assist in the determination of migration paths of shrimp to and from the estuaries and may be useful in predicting their abundance and distribution.

Although it could hardly be considered a technique for the indirect detection of fish stocks, the use of spacecraft for data transmission opens an entirely new area of appli cations of spacecraft to fishery research. One such system, Interrogation, Recording, and Location System (IRLS) will be capable of interrogating thousands of separate surface units placed at random, accurately fixing their position and recording data from them twice a day (fig 12). IRLS could provide the scientist with a means of obtaining surface and subsurface data from instrument buoys, ships, and aircraft. Coverage of this sort would complement the broad surface coverage by sensors carried in an orbiting spacecraft as well as provide surface calibration.

4 FUTURE APPLICATIONS

The use of spacecraft for fishery research must certainly challenge the imagination of marine scientists. The small effort put forth so far in effectively utilizing this tool is miniscule when compared to its potential. An example of possible future applications indicates where in an integrated data collection system, spacecraft may play an important role.

It is not too difficult to envision a global fishery forecasting network in which space-collected data will play an integral part. Earth-orbiting spacecraft with "phenomenon" sensors would isolate those areas of the world ocean which are apparently productive. This information would be relayed to a global fish-forecasting center and analyzed, in real time, to adjust for spatial and temporal disparities resulting from such things as variations in feeding patterns among different species of fish. Immediately, instructions would be relayed to the spacecraft to remotely "zoom" in on the area of interest.

The back-up "fish" sensors employed in the "zoom" technique would have much greater resolution and definition ability and would isolate specific surface or possibly subsurface fish schools. Repeated coverage would enable the determination of the movement and migration patterns so that once identified, the fish could be accounted for at all times. The new information from the "fish" sensors would also be relayed back to the global forecasting center where, based on certain parameters, the quantification and identification of the species could be made.

Essential to the system would be an inexpensive "black box" on each commercial fishing vessel to enable the fishermen to receive from the spacecraft information on the most productive fishing areas.

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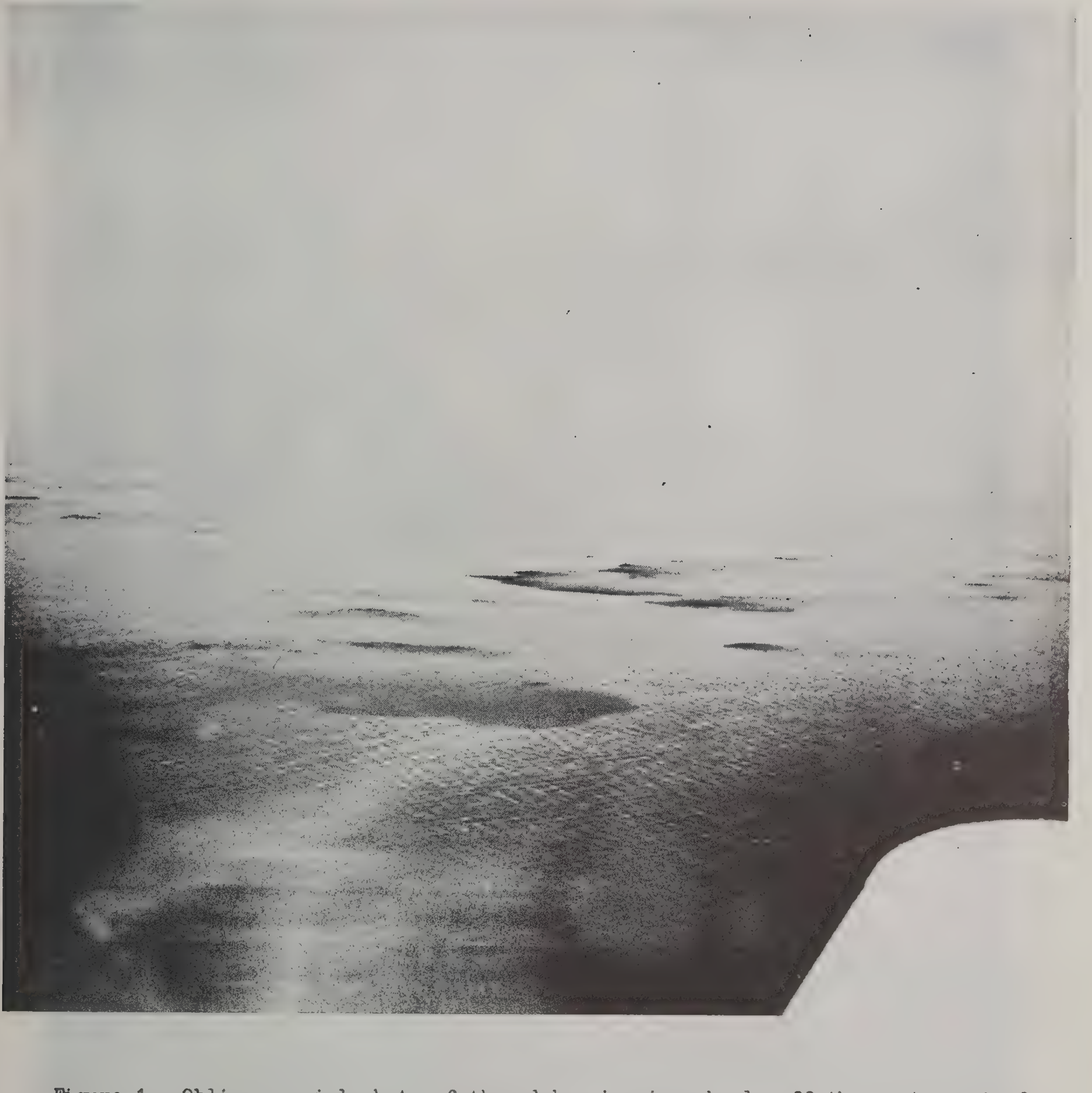


Figure 1.--Oblique aerial photo of thread herring in schools off the west coast of Florida. Photo taken from 2500 ft altitude using aerial Ektachrome film; (Bullis, Bureau of Commercial Fisheries).

Figure 2.--Vertical aerial photo of submerged anchovies leaving a wispy trail behind the school. White (almost invisible) object above school is a porpoise. Photo taken from 3,000 ft. altitude using aerial Ektachrome film; (Bullis, Bureau of Commercial Fisheries).

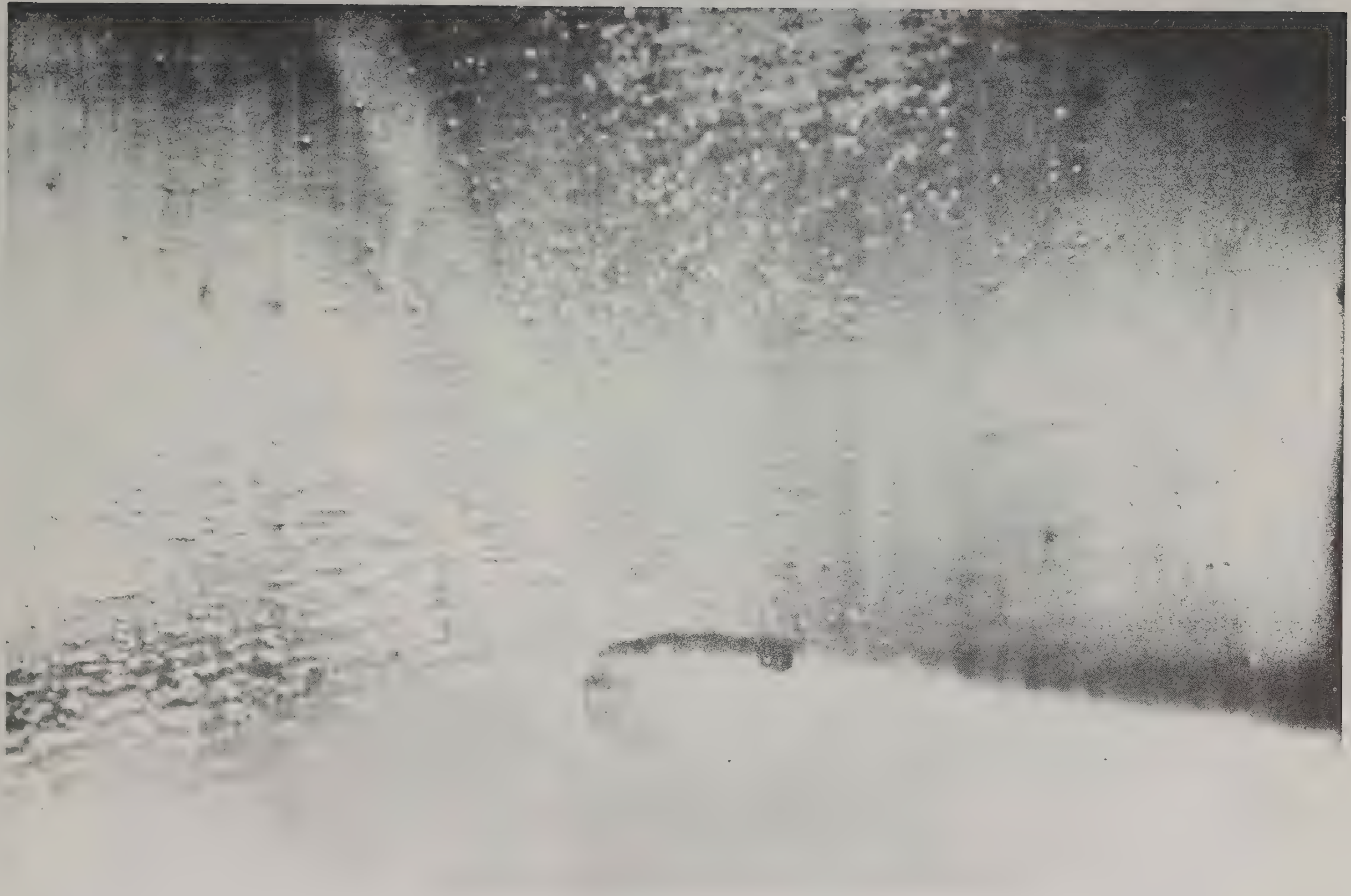


Figure 3.--Vertical aerial photo showing another example of unusual shapes fish schools assume. Photo taken from 2,500 ft altitude using aerial Ektachrome film; (Bullis, Bureau of Commercial Fisheries).

Figure 4.--Black and white copy of a false color analysis of the fish school in fig 2; (Ross, Philco-Ford Corp.)

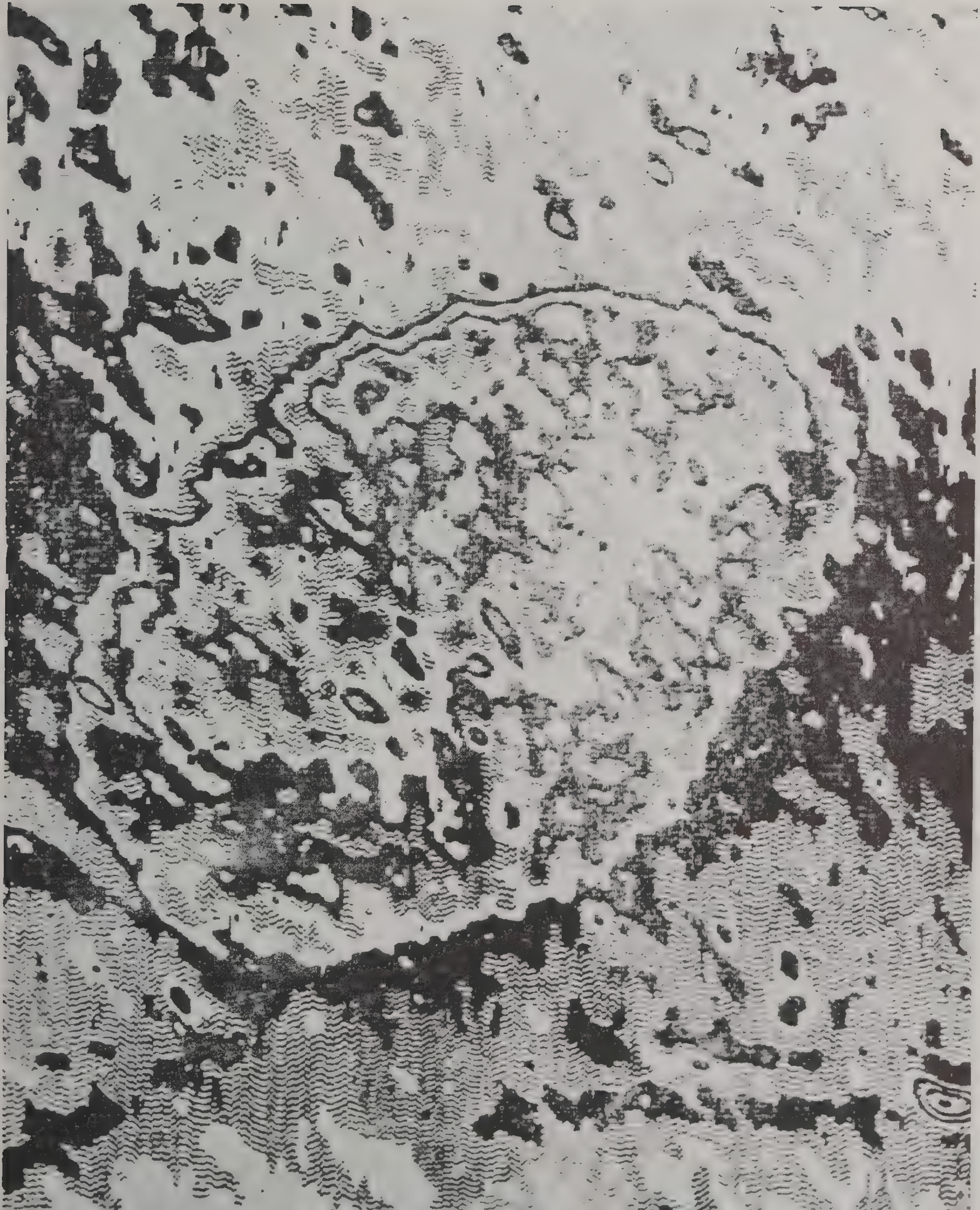


Figure 5.--Isodensitracing of microdensitometer analysis of fish school shown in fig 2; (NASA, MSC Houston).

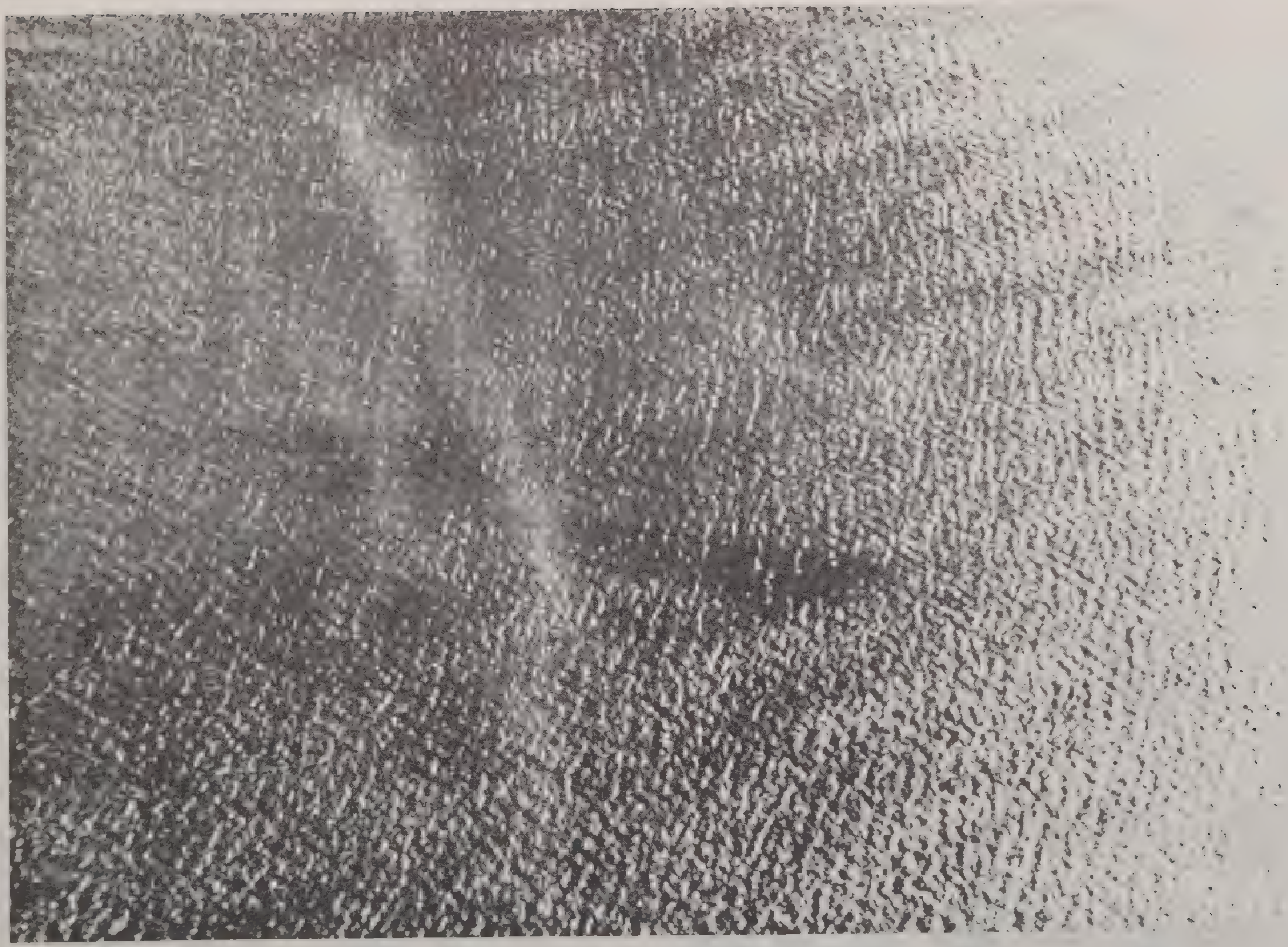


Figure 6.--Large fish oil slick photographed off the west coast of Florida. Photo taken from 3,000 ft altitude; (Barringer, Barringer Research Ltd.).

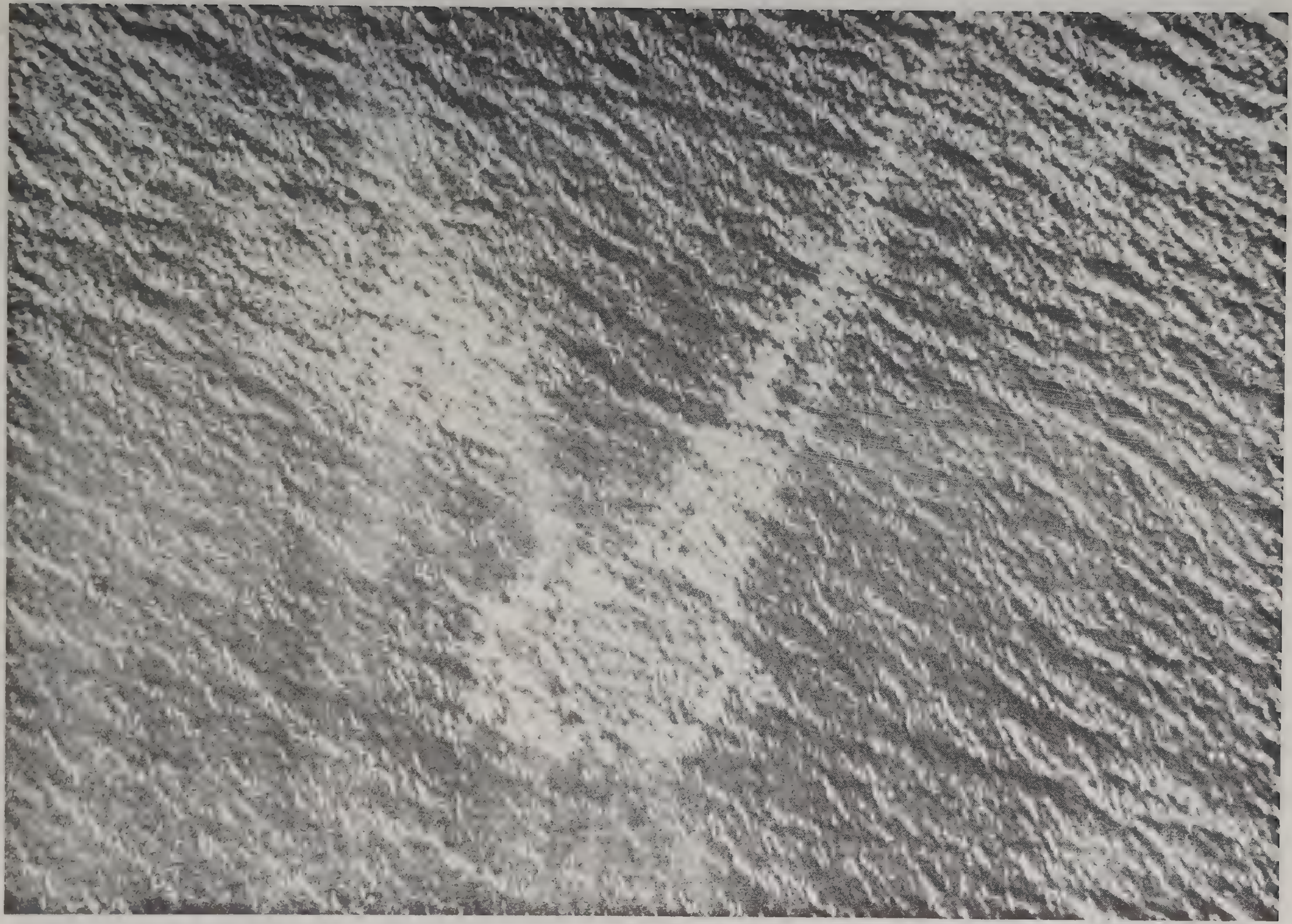


Figure 7.—Mineral oil slick photographed off the west coast of Florida. Photo taken from 3,000 ft altitude; (Barringer, Barringer Research, Ltd.).

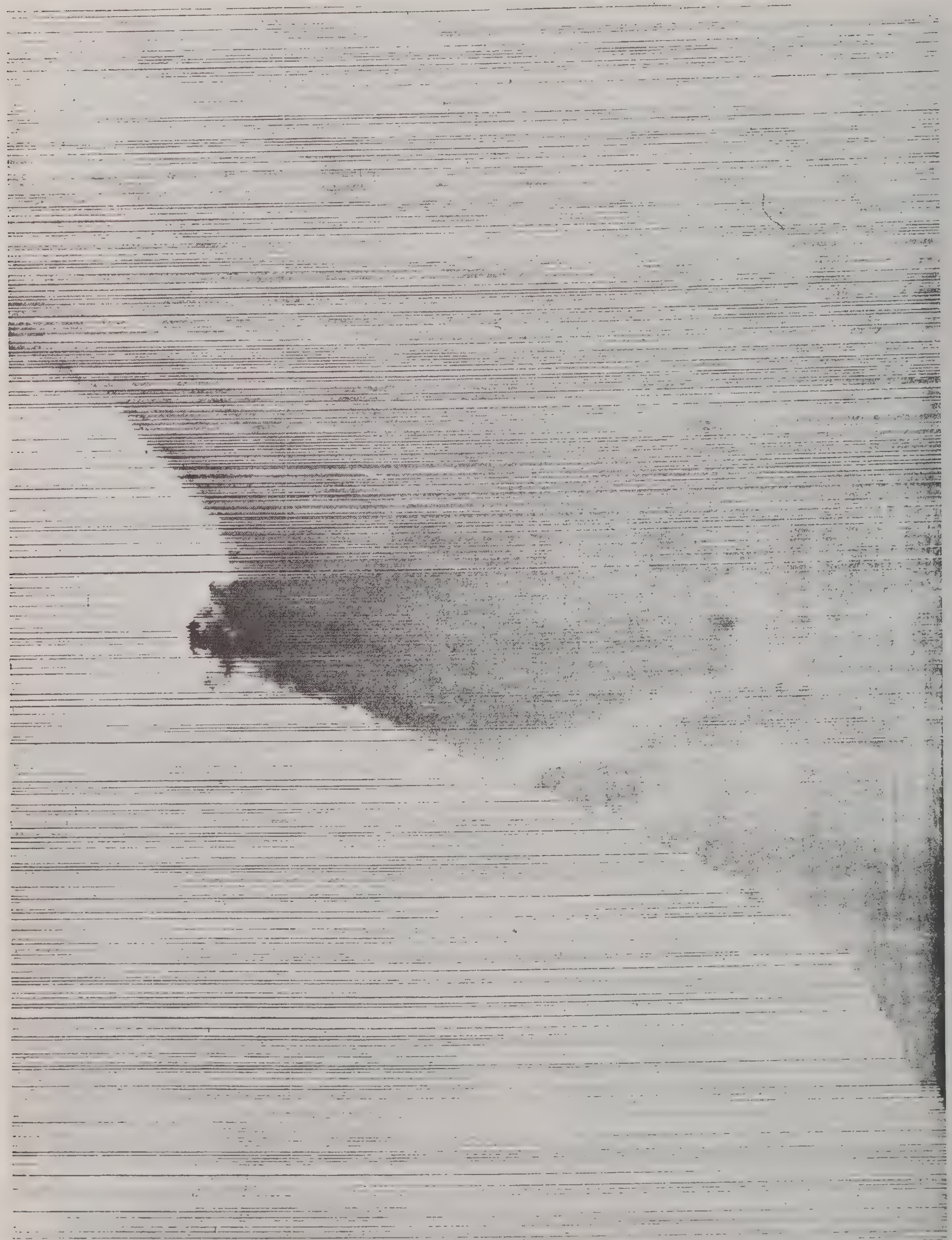
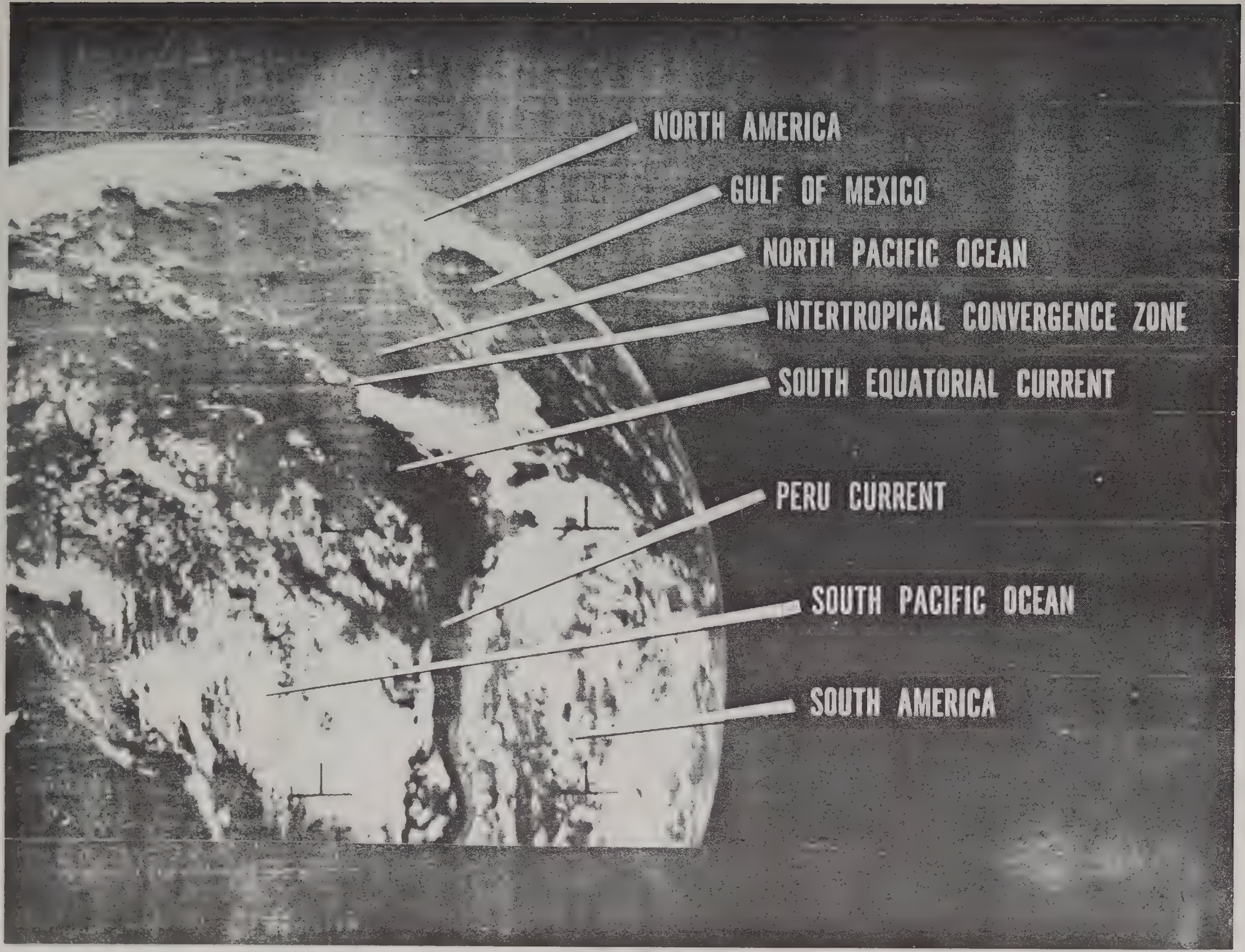


Figure 8.--Western boundary of the Gulf Stream off Cape Hatteras as defined by infrared imagery. The complex meanders of the boundary are easily identified; temperature differences often reach 8-10 C° between the warmer (darker) and colder (lighter) water; Wilkerson, NAVOCEANO).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GULF OF MEXICO
NORTH PACIFIC OCEAN
INTERTROPICAL CONVERGENCE ZONE
SOUTH EQUATORIAL CURRENT
PERU CURRENT
SOUTH PACIFIC OCEAN
SOUTH AMERICA

Figure 9.--ATS I spacecraft photograph of eastern Pacific Ocean showing cloud patterns and their relationships to major ocean current systems. Photo taken from spacecraft in an earth-synchronous orbit 36,000 kilometers over the Equatorial Pacific Ocean at 151° West longitude, April 10, 1967; (LaViolette, NAVOCEANO).

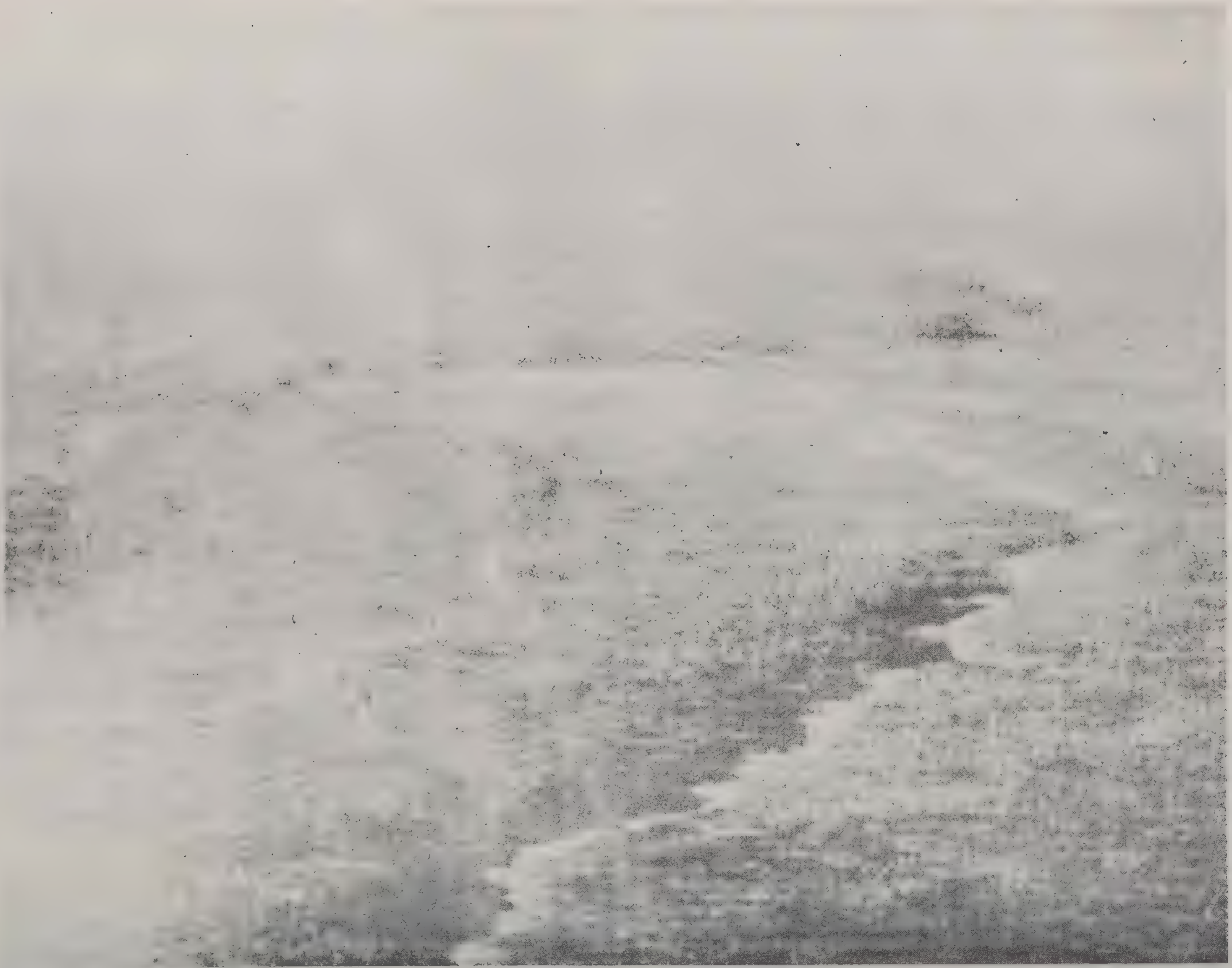
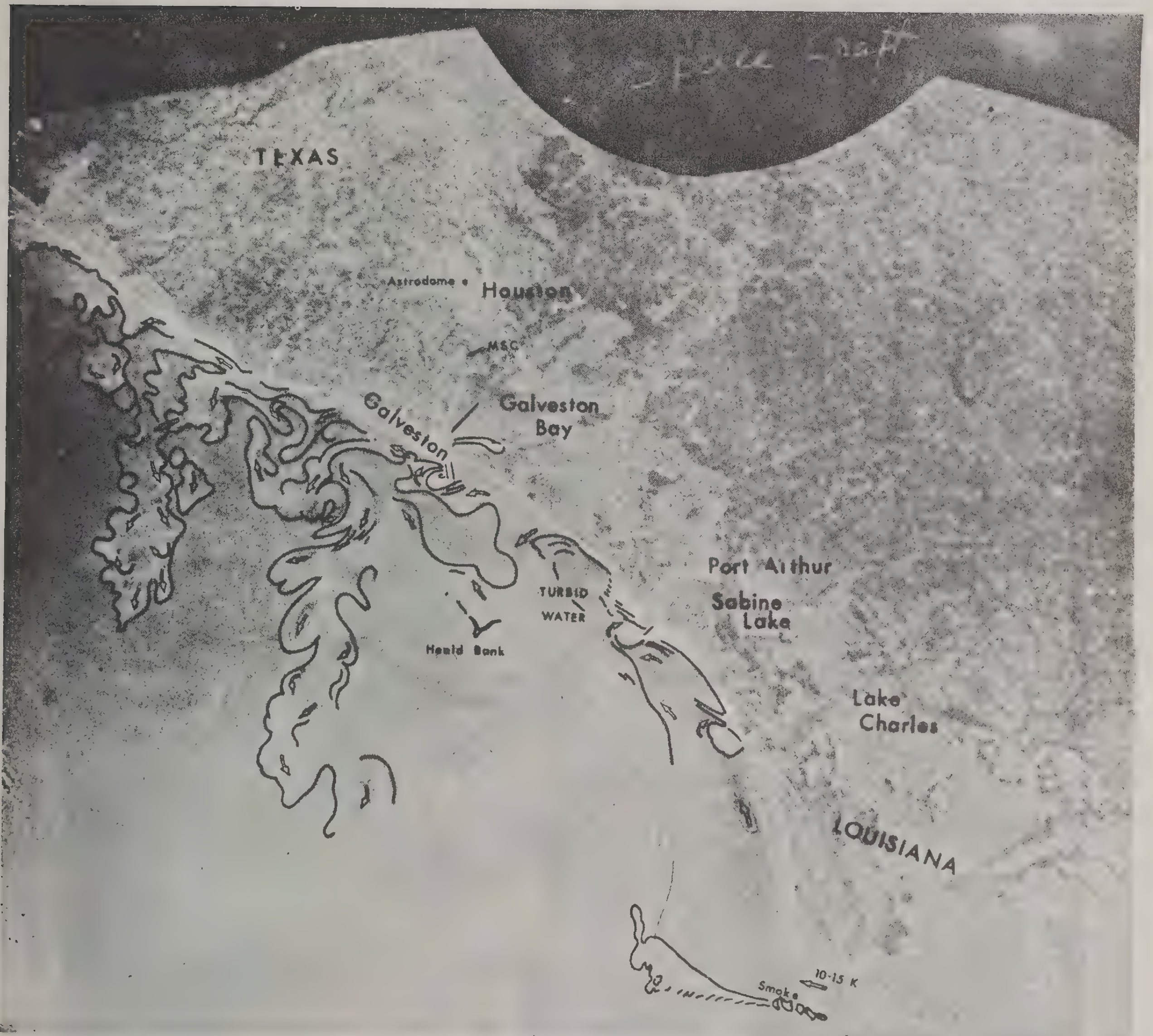


Figure 10.--Oblique aerial photo of meandering boundary of the Gulf Stream. Variations in color are indicative of the strong current shear between the shelf water and the Gulf Stream; (NAVOCEANO).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Lake
Charles
LOUISIANA
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Figure 11.--Oceanographic analysis of GEMINI XII photo. Original color photo was taken by astronauts Lovell and Aldrin, November 14, 1966 at 1300 local time; (Stevenson, Bureau of Commercial Fisheries).

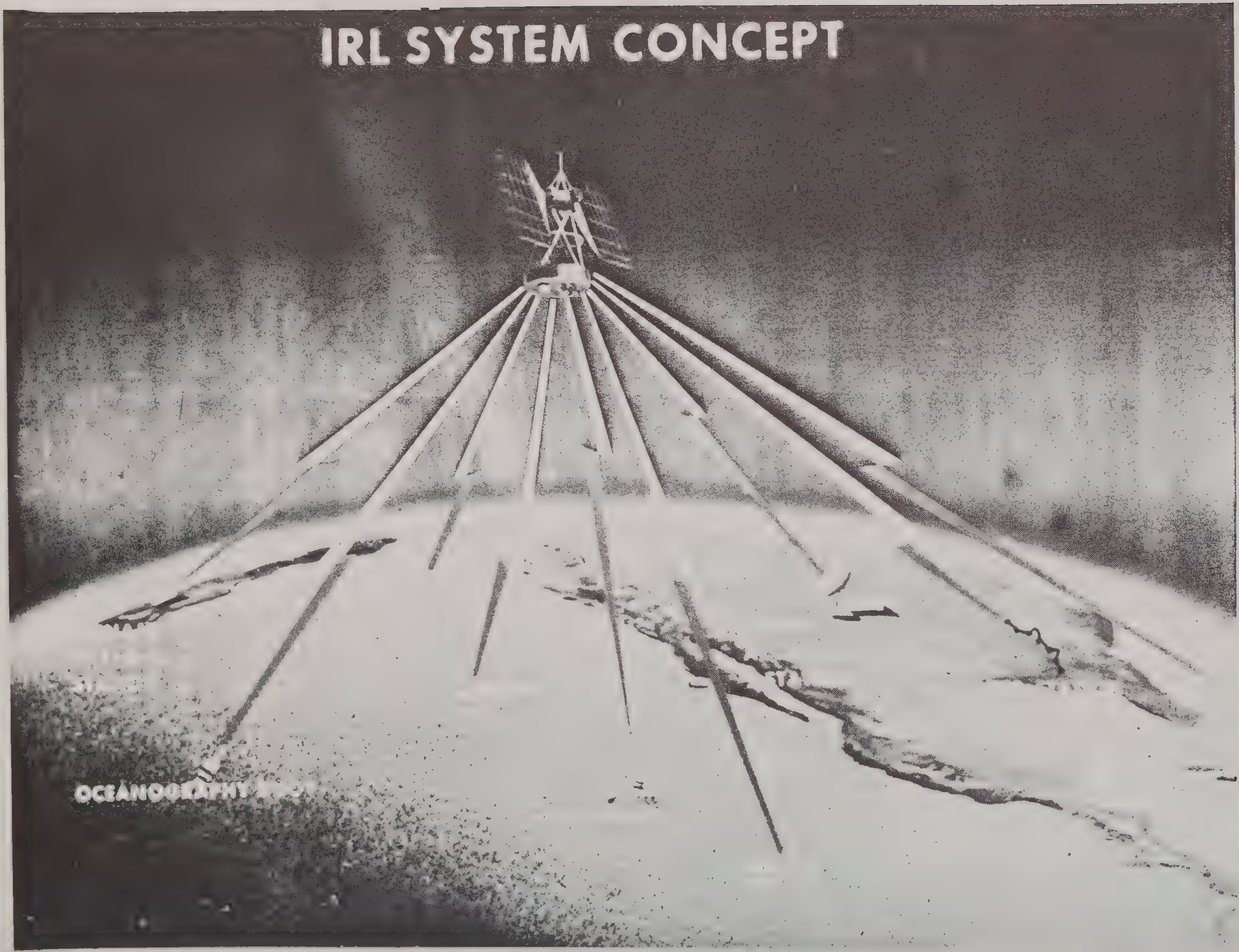
IRL SYSTEM CONCEPT
OCEANOGRAPHY

Figure 12.--Interrogation, Recording and Location Spacecraft System applied to oceanography; (NASA, Goddard).

Journal of Geophysical Research Vol. 73, No. 18, September 15, 1968

Eastward Flow within the South Equatorial Current in the Eastern South Atlantic[1]

P. A. Mazeika[2]

Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries
Miami, Florida 33149

Structure of the upper 500 m of the South Equatorial Current has been investigated in the eastern tropical Atlantic between latitudes 2°S and 7°S. The vertical distribution of east-west components of geostrophic velocities along longitudes 15°W and 20°W were computed for the two main seasons using the data of Equalant I and II. The velocity distribution shows a narrow eastward-flowing current centered near 4°S. The maximum velocity of 30 to 60 cm/sec was at about 150 meters in these sections, and in one section it appeared as a narrow eastward-flowing current having a maximum velocity at the surface. Geopotential topography of the 75-decibar surface, relative to 600 decibars, indicates that the narrow eastward-flowing current turns to the southeast at about 15°W and crosses the zero meridian at 12°S. The eastward-flowing current shows somewhat higher salinity, lower temperature, and higher oxygen content at the corresponding depths than the westward-flowing mass of the South Equatorial Current. The surface water in the zone of the westward flow (northern branch of South Equatorial Current) has no, or only weakly developed, maximum salinity core. The strong maximum salinity core on both sides of this zone is of a different origin.

The South Equatorial Current in the Atlantic is usually shown on surface current charts as a broad, rather constant westward flow between 3°N and 20°S [*Meteorological Office*, 1954; *U. S. Navy Hydrographic Office*, 1962; and pilot charts of the U. S. Navy Hydrographic Office]. Vertical sections of computed relative (geostrophic) velocity, however, show that the current may be more complex than the various representations of surface flow suggest.

Zones of eastward advection in an area formerly characterized by a basically westward flow have recently been described. *Reid* [1964] described a slow eastward flow from the surface to 500 meters and between 5°S and 12°S; the maximum velocity of 9 cm/sec was observed at 200–250 meters. *Metcalf et al.* [1962] showed a narrow, strong, and shallow (not more than 100 meters deep and 50 nautical miles wide) eastward-flowing geostrophic current between 2°S and 3°S along 13°30′W.

A satisfactory distribution of data for presentations in this paper was provided by the surveys of the International Cooperative Investigations of the Tropical Atlantic (Equalant I and II) in 1963-1964 [*Austin*, 1965]. Vertical sections of relative velocities along 15°W and 20°W were computed with reference to the 600-decibar surface; hatching indicates westward flow, and velocities are shown in centimeters per second.

A section from data taken between 6°N and 6°S during the summer season (Equalant II) is shown in Figure 1; computations of relative velocities for the zone of 2° of latitude south and north of the equator were not made because the geostrophic approximation is inadequate in the equatorial region. An eastward-flowing undercurrent appears between 3°S and 5°S, and the maximum velocity core is centered at about 4.5°S, at a depth of 160 meters. A westward flow from the surface to about 60 meters is interrupted by a rather narrow zone of eastward flow between 4°15′S and 5°S.

Between 3°N and 4°N, the Equatorial Countercurrent is well marked from the surface to about 100 meters. The cell of westward flow in the surface layer between 4°N and 5°N and a cell of weak eastward flow, below 125 meters, at 3°N are probably merely areas of slow motion; the actual direction cannot be reliably obtained by computation of the relative gradient flow.

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[1] Contribution 63, Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami, Florida 33149.

[2] Now at the U. S. Naval Oceanographic Office, Code 7240.

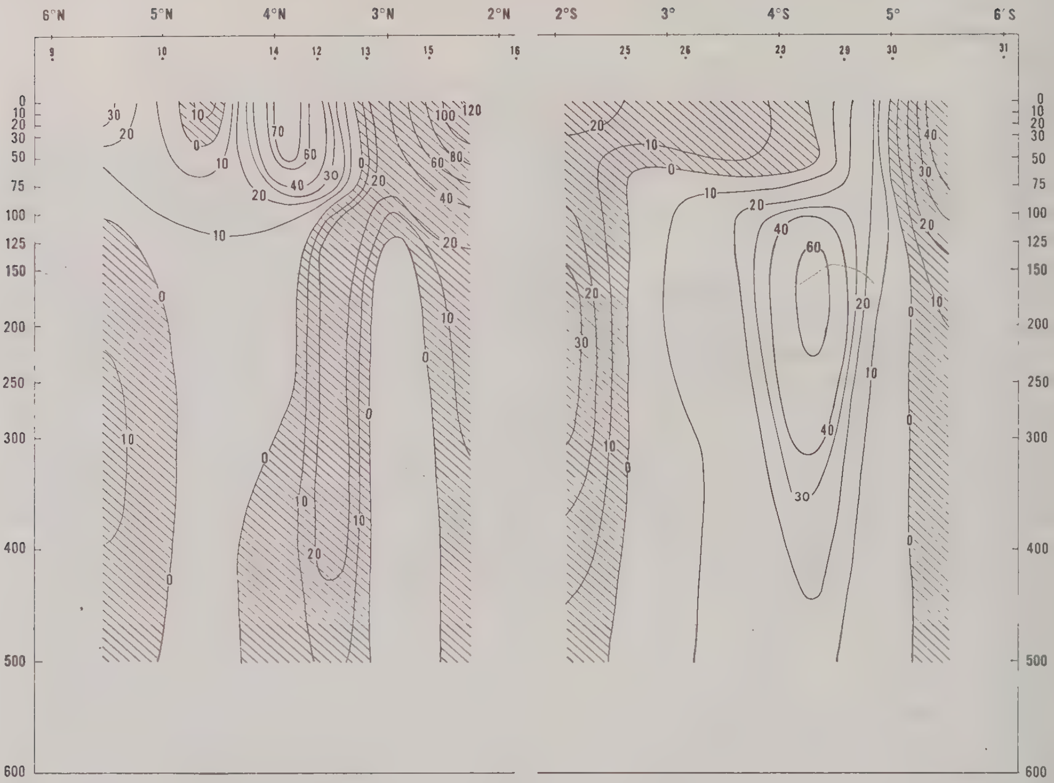


Fig. 1. East-west components of geostrophic velocity in centimeters per second along 20°W, relative to 600 decibars. Westward-flowing currents hatched. *Pillsbury,* September 3–10, 1963.

The vertical distribution of salinity for the same section (Figure 2) shows three salinity maximums. The northern high-salinity tongue is associated with the Equatorial Countercurrent and is separated from the high-salinity core of the Equatorial Undercurrent. A core of relatively high salinity in the Equatorial Undercurrent is evident on both sides of the equator at about 60 meters depth.

The southern high-salinity tongue was associated with the South Equatorial Current south of 5°S and was also separated from the high-salinity core of the Equatorial Undercurrent in a zone of westward-flowing current north of 3°S, approximately. Separation of the high-salinity cores may be an indication of vertical mixing in the zone of separation. The undercurrent at 4°S is characterized by a dip of isohalines showing that the salinity is somewhat higher within the eastward-flowing mass. However, the upward slope at the isohalines is within the right flank of the current. The salinity is considerably lower in the southern branch of the South Equatorial Current, and apparently intense horizontal mixing occurs in the boundary region.

During Equalant II (Figure 3), this eastward subsurface flow was seen as a narrow current in the geopotential topography for the 75-decibar surface, relative to 600 decibars. The trough in dynamic topography, coinciding approximately with the eastward flow in the vertical *Pillsbury* section, is rather consistent in all available sections. The flow moves along 4°S, turning southeast near 14°W. This may not be the same as the eastward flow described by *Reid* [1964]. The eastward transport shown in Figure 3 between 7°S and 12°S approximates the position of the current described by Reid, but the transport is separated from the narrow eastward-flowing current by a westward-flowing current at 6°S. During the South Atlantic summer, the eastward flow at 4°S may extend farther

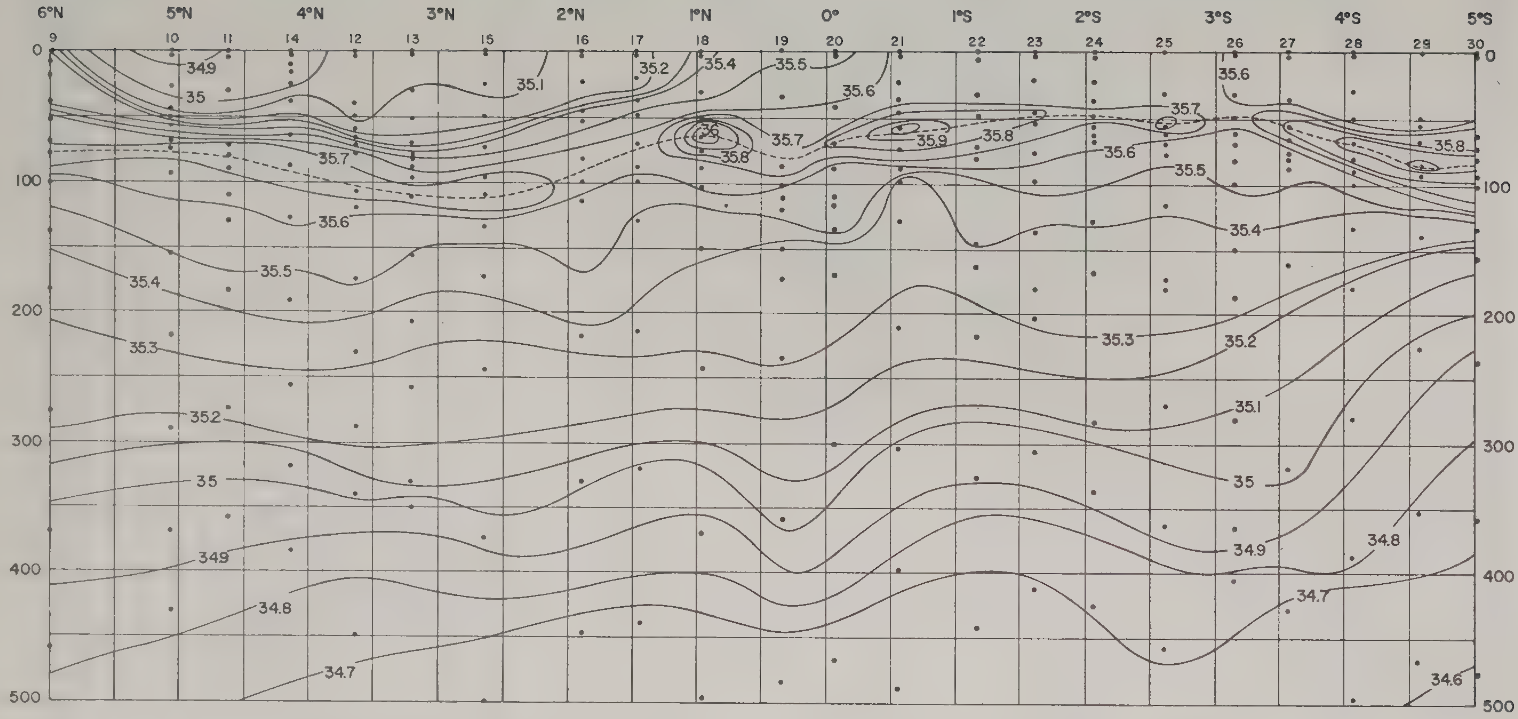
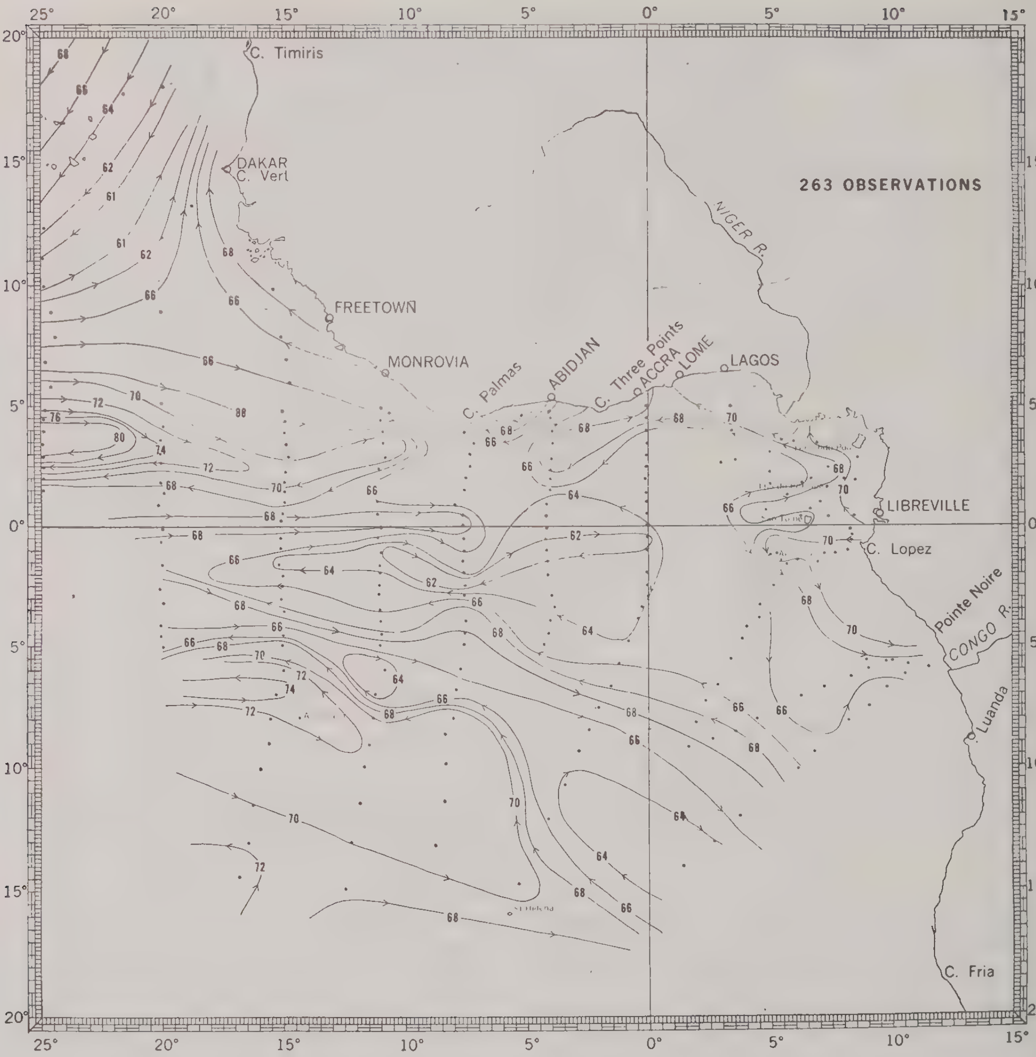


Fig. 2. Salinity at 20°W (‰). Cold season. *Pillsbury*, September 4–9, 1963. Depth in meters. Dashed line shows maximum; dots show observation points.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C. Lopez
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CONGO R.
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Fig. 3. Geopotential topography of the 75-decibar surface, relative to 600 decibars in dynamic centimeters. Cold season (July, August, September).

east before turning southeast. *Williams* [1966] obtained, with Equalant I data, the geostrophic eastward flow at 50 meters along latitude 3°S to 4°S between the 10°W and 7°W meridians.

Three relative velocity profiles are drawn from data collected during the southern hemisphere summer (January, February, March, and April, Equalant I). The transects were centered near 15°W and were separated by about 20-day intervals. An eastward-flowing undercurrent is evident in Figure 4 at 4°S. The vertical continuity between the strong narrow surface current and the wider subsurface flow is uncertain.

The vertical salinity distribution (Figure 5) along the section shows a continuous tongue of high salinity. It spreads from the southern limits north to 3°S, approximately. The salinity core in the Equatorial Undercurrent is near the velocity maximum [*Metcalf et al.*, 1962], but a different situation seems to exist along the tongue of high salinity of South Atlantic origin. This tongue apparently spreads along the layer of minimum velocity. The core probably could not cross the eastward flow without being disrupted by vertical mixing if the eastward flow were continuous from the surface downward.

The zone of weak salinity maximum (separating two salinity cores of different origin) is in a continuous westward flow from the surface to below 500 meters, between 2°S and 3°S, whereas above the tip of the high-salinity tongue the westward surface flow extends to 4°S, approximately.

Vertical distribution of gradient velocities along the next section (Figure 6), taken 20 days later, shows that the eastward flow centered at 4°S is a stronger undercurrent than it is in the previous section (Figure 4).

The northern branch of the South Equatorial Current, separating the Equatorial Undercurrent from the eastward flow at latitude 4°S, has a velocity maximum at the surface and another between 125 and 300 meters. A current of similar structure was also present at the first section, 20 days earlier; however, the subsurface velocity core was considerably less developed. This northern branch of westward transport is quite powerful and is probably the main artery of the South Equatorial Current.

The shallow eastward flow between 6°S and 7°S is somewhat shallower and about 1° farther south than it is in the previous section (Figure 4).

The two *Explorer* sections are rather similar. The southern branch of the eastward flow at the surface is repetitive and probably permanently

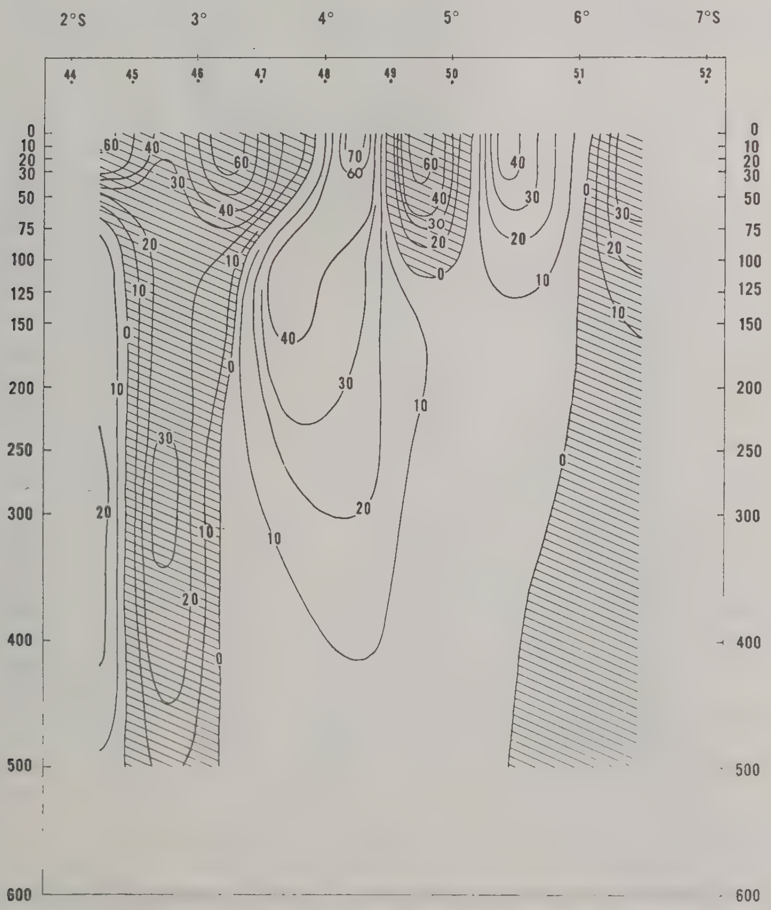

Fig. 4. East-west components of geostrophic velocity in centimeters per second along 15°W, relative to 600 decibars. Westward-flowing currents hatched. *Explorer,* March 2–4, 1963.

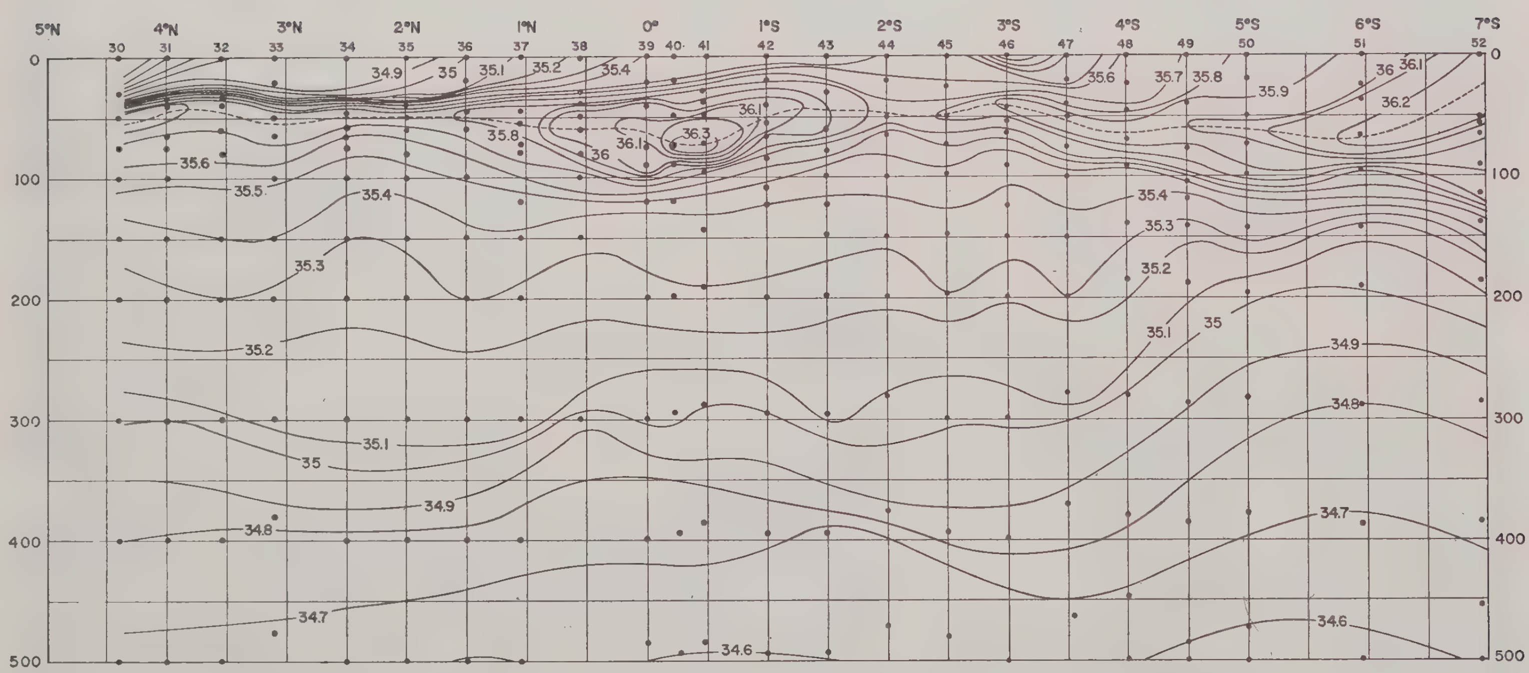

Fig. 5. Salinity at 15° W(‰). Warm season (January, February, March, April). *Explorer*, February 24–March 4, 1963. Depth in meters. Dashed line shows maximum; dots show observation points.

present. The two branches of the South Equatorial Current are in about the same zones in both sections. Separation of surface and subsurface eastward-flowing currents at 4°S in the second section may be an indication that the separation occurred in the first section also, since the salinity core was not disrupted.

The tongue of salinity maximum of the second *Explorer* section (Figure 7) extended northward at the depth of low velocity right below the two shallow surface currents flowing in opposite directions. The shallow eastward flow is between 6°S and 7°S. The westward flow, having significant velocities to a depth of about 60 meters is between 4°S and 6°S, and another shallow eastward flow is between 3°S and 4°S. The northern branch of the westward flow is north of 3°S.

Twenty days after the second *Explorer* section, a third section along 15°W was made by *Zvezda* (Figure 8). In this section the undercurrent at 4°S was narrow, but its maximum velocity was still at about 150 meters. The eastward flow, centered at about 6°S, which was quite shallow in the two previous sections, developed into a rather deep and broad eastward-flowing current spreading northward at depths of 150 to 400 meters. Here it seems that another subsurface current may be developing which is shown as a continuous eastward flow between

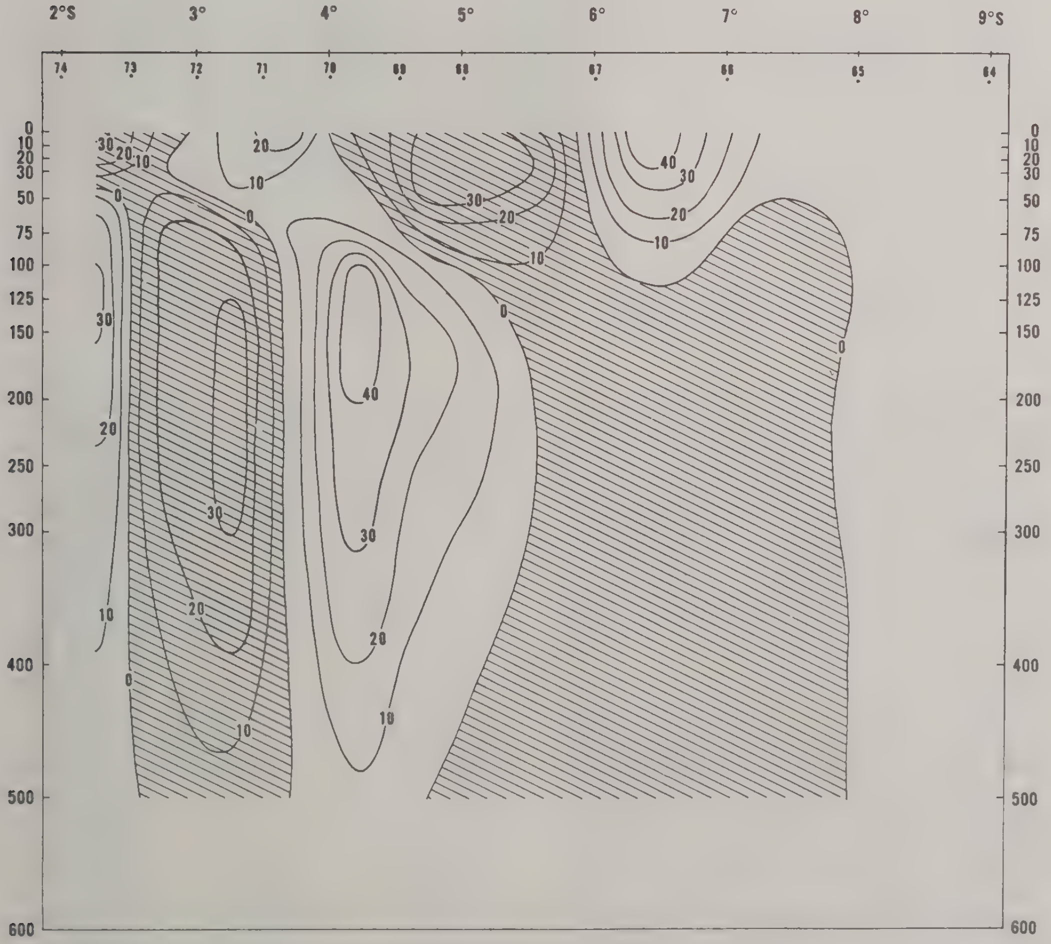

Fig. 6. East-west components of geostrophic velocity in centimeters per second along 15°30′W, relative to 600 decibars. Westward-flowing currents hatched. *Explorer*, March 21–24, 1963.

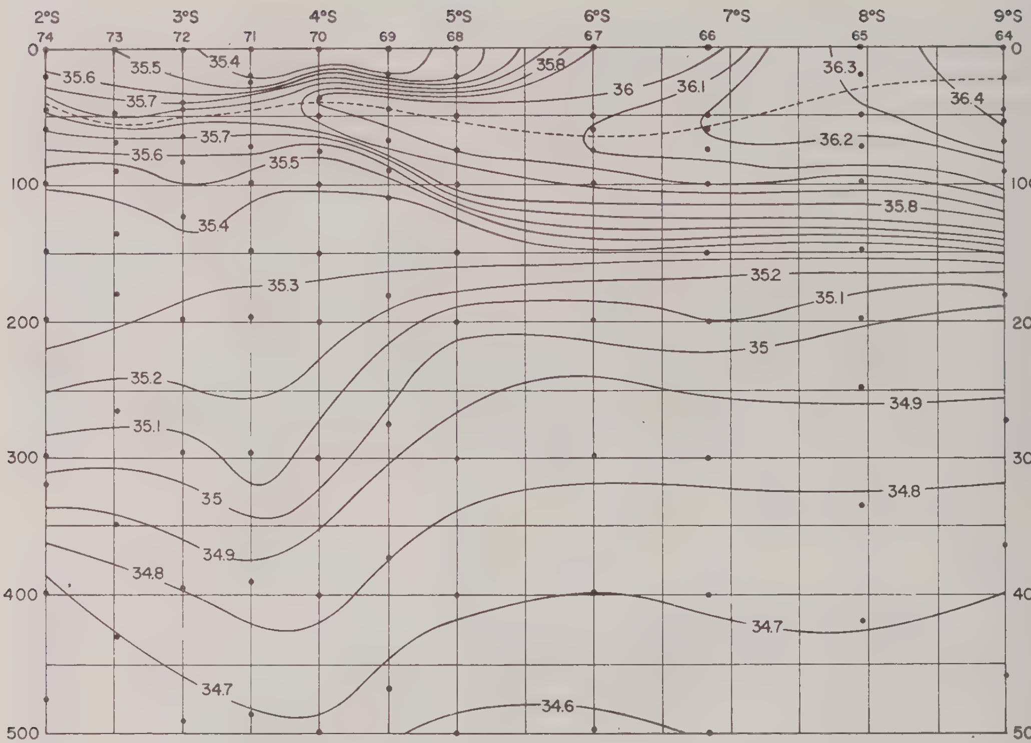

Fig. 7. Salinity at 15°30′W (‰). Warm season. *Explorer*, stations 64–74, March 21–24, 1963. Depth in meters, Dashed line shows maximum; dots show observation points.

the surface and subsurface. However, a continuous maximum-salinity tongue stretched almost to 4°S at about 75 meters depth, and there probably was a discontinuity of eastward flow in this layer. The vertical salinity distribution of this transect was basically similar to the salinities shown in Figure 2, 5, and 7.

Volume transport of the eastward flow at 4°S in the four sections were: *Pillsbury*, 20 × 10^6 m^3/sec; first section of *Explorer*, 13 × 10^6 m^3/sec; second *Explorer*, 12 × 10^6 m^3/sec; and *Zvezda*, 5 × 10^6 m^3/sec. There is a considerable variation of transport, latitude, depth, and width at the eastward flow among the four sections. Some of the differences may be due to data errors, but it is possible that the cells of eastward flow are not very constant with respect to size and position.

Mean temperatures and concentrations of dissolved oxygen at 150 meters depth between the equator and 6°S are shown in Table 1. The means were computed from the data illustrated in Figures 1, 4, 6, and 8 for a depth of 150 meters, which is within the velocity core of the undercurrent. The temperatures appear to be about 0.5° lower in the undercurrent than in the northern branch of the South Equatorial Current and about 2° lower than in the southern branch. The oxygen content is slightly higher in the eastward subsurface flow than in both branches of the South Equatorial Current. The salinity is higher in the undercurrent, but the isohalines slope sharply upward in the right flank of the eastward flow (Figures 2, 5, and 7).

In most of the sections the eastward-flowing filament at 4°S can be considered an undercurrent. The main transport of this current, shown in Figures 1, 4, 6, and 8, is between 100 and 200 meters. Together with the Equatorial Countercurrent at the surface (Figure 1) and the Equatorial Undercurrent with maximum transport at about 60–70 meters [*Metcalf et al.*, 1962], this southern hemisphere undercurrent is a part of a complex of equatorial, eastward-

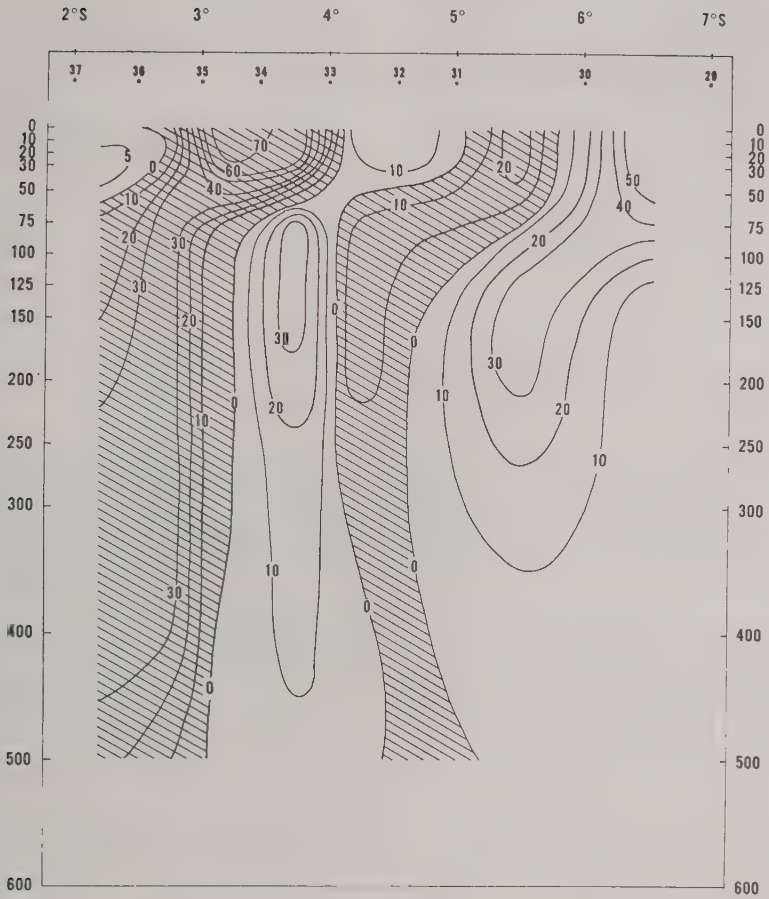

Fig. 8. East-west components of geostrophic velocity in centimeters per second along 15°W, relative to 600 decibars. *Zvezda,* April 11–14, 1963. Westward-flowing current hatched.

flowing currents having a stepwise increase in depth, from north to south, of the main transport.

The repetitive pattern of eastward flow within the South Equatorial Current in four sections during two seasons indicates that such a flow may be a permanent feature. The data, however, are not adequate to allow us to investigate the structure, origin, and stability of these currents in detail.

TABLE 1. Mean Temperature and Oxygen Content at 150 Meters Depth

Latitude	T, C°	O_2, ml/l
0°	14.10	3.55
1°S	14.11	2.81
2°S	13.57	2.75
3°S	13.58	2.50
4°S	13.10	2.69
5°S	13.46	3.05
6°S	15.28	2.54

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revised June 6, 1968.)

Influence of the Komandorskiy Ridge on Surface and Deep Circulation in the Western North Pacific Ocean

by

W.B. McALISTER, F. FAVORITE, and J. INGRAHAM
Bureau of Commercial Fisheries Biological Laboratory
Seattle

Data are presented from a series of hydrographic stations taken from the R/V George B. Kelez during February and March 1966. Observations from 18 of the 34 stations extended below 4,000 m. Stations were taken in eight crossings of the Komandorskiy Ridge (northern extent of Emperor Seamount Chain) between lat. 45° and 53°N. The data have been compared with previous deep stations in this region and with a model of the general circulation in the North Pacific Ocean.

The Komandorskiy Ridge extends southward from the Komandorskiy Islands; it lies almost normal to the westward flow of the Alaskan Stream and the eastward flow which results from the confluence of the Kuroshio and Oyashio Currents. The Komandorskiy Ridge marks the westernmost extent of the Alaskan Stream as a well defined feature, the Alaskan Stream being deflected mainly to the north at the ridge. The Kuroshio-Oyashio flow shows little disturbance, but the presence of the ridge appears to inhibit any deep circulation in this region.

Previous summer observations in this region showed similar flow; the observed distributions and transports are consistent with a generalized model circulation in the North Pacific Ocean.

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An Electric Beam Trawl for the Capture of Larval Lampreys[1]

INTRODUCTION

The chemicals used to control the sea lamprey, *Petromyzon marinus,* in the Great Lakes (Applegate, Howell, Moffett, Johnson, and Smith, 1961) have drastically reduced populations of larval lampreys in tributary streams. These larvicides are too costly and difficult to apply, however, in inland lakes, estuaries, and bays. Populations of sea lampreys in these areas constitute a threat to the refinement of the control.

The gear available to locate, sample, and evaluate larval populations in deep water are inefficient. Electric shockers (Stauffer and Hansen, 1958; Braem and Ebel, 1961), satisfactory for collecting ammocoetes in streams, are limited to shallow water. The use of mechanical devices such as the Petersen dredge, anchor dredge (Thomas, 1960), and the orange-peel dredge is time consuming, inefficient, and relatively ineffective in providing reliable quantitative evaluation of population size and composition over large areas of bottom.

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A device was required to sample adequately many areas in a short period of time, regardless of the depth of water. Mobility also was essential to permit operation of the unit in the various Great Lakes and in inland waters. An electrified beam trawl has been developed that most nearly meets these requirements. It has been used successfully to collect larvae of the sea lamprey, American brook lamprey (*Lampetra lamottei*); northern brook lamprey (*Ichthyomyzon fossor*), and silver lamprey (*I. unicuspis*). Effectiveness of the trawl did not appear to differ with species.

THE BEAM TRAWL AND ELECTRODE ARRAY

The electric beam trawl combines a sled-mounted net, based on the typical design illustrated by Sundstrom (1957), with an electric field. The U-shaped sled runners are constructed of 3-inch-wide strap steel; they are 3 ft long and about 18 inches high. The runners are separated by two 5-ft lengths of galvanized pipe, 1-¼ inches in diameter (Figure 1). Adjustable extensions are mounted vertically to a supporting bar between the top and the base of the runners to accommodate nets of different depths.

The net, which is made of ¼-inch-bar nylon netting, has a 5- by 2-ft mouth, and tapers to 1 ft in width and 2 ft in height at the cod end. A funnel, attached inside the net to prevent escape of larvae, has an opening of 3 × 2 ft, and tapers to 6 × 6 inches. Six feet of the cod end are lined with saran screening, 14 × 18 meshes to the inch. The screen retains ammocoetes as short as 30 mm. A draw string permits the net to be emptied through the cod end.

The towing bridle is designed to accommodate the electrode array. Three equally spaced manila lines, attached to the front of the trawl sled, extend 10 ft to a 5-ft wooden spreader bar. From the spreader bar the lines converge to form a single towline.

The negative electrodes are attached to the two outer lines of the bridle and the positive electrode is fastened to the center line. The negative arrays extend from the spreader bar 7 ft toward the sled. The positive electrode begins 2 ft from the spreader bar and extends to the sled. Added surface area for the positive electrode is provided by a section of ⅛-inch-mesh hardware cloth between the two crossmembers of the sled.

The electrodes consist of No. 10 stranded copper wire wrapped around the manila lines. Six-inch sections of brass sash chain are fastened to the copper wire at 1-inch intervals to increase electrode surface area. Electric power is supplied to the electrode array through a 2-wire, No. 12, waterproof conductor attached to the manila towline.

THE TOW BOAT

A fiberglass Boston whaler[2] with an overall length of 17 ft and a beam of 6 ft, 2 inches, and powered by a 75-horsepower outboard motor, was selected as a tow craft (Figure 2). The fiberglas hull was preferred because its insulating qualities lessened the hazards from electric shock. The boat met most requirements. It has a large load capacity with a rated reserve buoyancy of 2,000 pounds, and the hull design provides a comparatively stable work platform. The craft is considered seaworthy enough for safe operation on the inshore waters of the Great Lakes, yet it can be transported easily by trailer.

APPLICATION OF ELECTRICITY TO THE TRAWL

The trawl's electrode array is energized by a square-wave generator. The input power is provided by a 2.5-kilowatt generator which supplies 3-phase, 180-cycle, alternating-current. The electronic unit produces nearly perfect square-wave pulses over the complete range of duty cycles and at any desired repetition rate up to 166 pulses per second.

Successful operation of the ammocoete trawl depends entirely on the electric field which stimulates lamprey larvae into an almost immediate emergence from their bur-

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[2] Trade names used in this publication do not imply endorsement of commercial products.

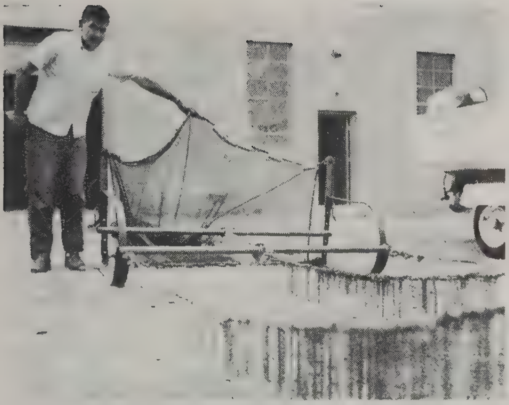

FIGURE 1.—The electrified beam trawl used to capture lamprey larvae in deep water.

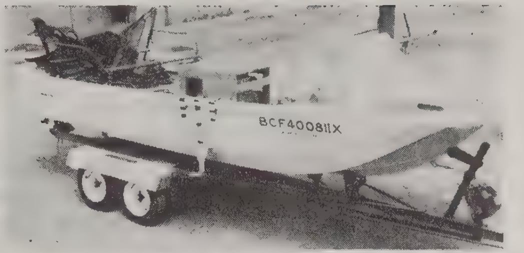

FIGURE 2.—The complete unit used to locate sea lamprey larvae inhabiting offshore waters. The detachable bracket on the side of the boat holds the transducer for the depth recorder. The large box amidship houses the generator that provides electric power.

rows and, preferably, holds them off the bottom and within the path of the net. Although many types of electric current will cause lamprey larvae to leave their burrows, most rapid emergence in limited laboratory tests was obtained with square-wave pulses of direct current. More than 90% of the ammocoetes left their burrows within 7 seconds when subjected to pulses of duration of 166 milliseconds at a frequency of 3 pulses per second. The results of a few trials conducted in streams with wild and undisturbed populations agreed with those from the laboratory.

In addition to obtaining rapid emergence by the larvae, it was desirable to contain them within the electric field until they could be swept into the net. Larval lampreys exhibit a leading response to interrupted direct current over a wide range of duty cycles and repetition rates, but the power level for larvae of different sizes is extremely critical. A slight change in voltage greatly alters the reactions of a larva. It was impossible, therefore, to obtain a uniform leading response from ammocoetes of all sizes in a natural population with a given level of power applied to the electrodes. Under these conditions, the efficiency of the trawl depends mostly on synchronization of emergence time with towing speed.

The effective area of the trawl's electric field varies inversely with the size of the ammocoetes. Larvae captured by the trawl ranged from 18 to over 180 mm total length. Large ammocoetes within 6 inches of the electrodes may be immobilized in their burrows, limiting the effective fishing area to a strip about 3 ft wide (2 strips, each 1-½ ft wide). At the same power level small larvae may emerge from burrows close to the electrodes but be undisturbed midway between the electrodes where the field is weakest.

Since electric current varies at different locations because of differences in conductivity of the water and bottom, the intensity of the electric field is established on the basis of power. In most locations as little as 300 watts of electric power have proved satisfactory. Fluctuations in bottom conductivity, which influence the amount of electric current reaching the ammocoetes, have not presented a problem. Fortunately, the conductivity of the water generally is uniform throughout a given area of a lake. Changes in the conductivity of the bottom are detected readily by an ammeter on the electronic unit and the power level is adjusted accordingly.

OPERATION OF THE TRAWL

The trawl is set and retrieved by hand. The set is made from the left side of the boat while the boat is making a sharp left turn. This procedure prevents the net from becoming fouled in the trawl sled or the outboard propeller. When the sled contacts the bottom, the boat is straightened out, and the towline is released at a ratio of about 4 to 1. The electrode array is energized and the towing speed of about 1 mile per hour is established.

Towing speed is controlled by a motor tachometer mounted on the control console. The effect of wind or water currents is periodically checked with a traveling wheel which can be attached to the side of the sled. The RPM of the wheel, recorded by an electric counter, provides a measure of the distance traveled and the rate of speed. The traveling wheel is not used continuously because it interferes with setting and retrieving the net.

The net is subject to tearing and to wear from abrasion. Occasionally it fills with bottom material when dragged over soft bottom. If the net becomes filled and cannot be retrieved, it can be emptied by pulling a floatline attached to the cod end.

EVALUATION OF THE TRAWL

A precise evaluation of the trawl's efficiency has not been obtained. In addition to problems inherent in an efficiency analysis of a mobile collecting device, the trawl depends on an electric field with all its variables. Attempts to evaluate the gear with laboratory facilities, mark-and-recovery techniques, and the release of known numbers of larvae in confined areas have proved inconclusive. These tests, however, as well as several attempts to compare the efficiency of the trawl with portable shockers, have shown that the characteristics of collections of ammocoetes taken with the trawl are very similar to those of samples taken with shockers and the larvicide. The length distribution of the larvae and the species composition of the catches were similar for trawls and portable shockers. Distribution records of ammocoetes, within a given area, were also similar for the two gears.

Experimental trawling in waters where information was available on the abundance of ammocoetes indicated that the catch rate of the trawl reflected relative abundance. In areas where abundance was known to be extremely high (about 0.2 larva per sq ft), the trawl captured larval lampreys at a rate of more than 15 per minute.

The ability of the trawl to measure the relative abundance of ammocoetes over a wide range of habitat conditions makes it a valuable tool to locate and assess ammocoete populations in the upper Great Lakes where it has been used since its development in 1961 (Great Lakes Fishery Commission, 1961–66).

OTHER FISH IN THE TRAWL

Although the electric trawl was not designed to capture fish other than larval lampreys (the spreader bar and electrode array would be expected to drive most fish from the path of the trawl), we captured many fish while we were trawling for ammocoetes. The following 23 species have been taken: alewife, *Alosa pseudoharengus*; American smelt, *Osmerus mordax*; northern pike, *Esox lucius*; blacknose dace, *Rhinichthys atratulus*; golden shiner, *Notemigonus crysoleucas*; common shiner, *Notropis cornutus*; spottail shiner, *Notropis hudsonius*; blacknose shiner, *Notropis heterolepis*; bluntnose minnow, *Pimephales notatus*; white sucker, *Catostomus commersoni*; brown bullhead, *Ictalurus nebulosus*; burbot, *Lota lota*; brook stickleback, *Culaea inconstans*; ninespine stickleback, *Pungitius pungitius*; trout-perch, *Percopsis omiscomaycus*; rock bass, *Ambloplites rupestris*; yellow perch, *Perca flavescens*; walleye, *Stizostedion vitreum vitreum*; sauger, *Stizostedion canadense*; logperch, *Percina caprodes*; johnny darter, *Etheostoma nigrum*; mottled sculpin, *Cottus bairdi*; slimy sculpin, *Cottus cognatus*.

The small bottom-dwelling species were most vulnerable to the trawl. Large numbers of logperch, johnny darters, and sculpins appeared in the catches. Invariably the catch of other species was limited to the smaller sizes, mostly fry or fingerlings. Deepwater tows (down to 110 feet) in Lake Superior produced large numbers of opossum shrimp, *Mysis relicta*.

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Bernard R. Smith, Field Supervisor for Sea Lamprey Control, Biological Station, Marquette, Michigan, suggested the use of electricity with a beam trawl for the capture of lamprey larvae.

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ALBERTON L. MCLAIN
FREDERICK H. DAHL

U. S. Bureau of Commercial Fisheries
Biological Station
Marquette, Michigan

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A Systematic Study of the Greenside Darter, *Etheostoma blennioides* Rafinesque (Pisces: Percidae)[1]

Robert Victor Miller

A study of infraspecific variation was based on more than 4000 specimens from approximately 540 series, taken throughout the range of *Etheostoma blennioides.* On the basis of scale and fin-ray counts, degree of opercle and belly squamation, size of upper lip tip, and presence of a distinct frenum, four subspecies are recognized: *E. b. blennioides* Rafinesque, *E. b. newmanii* (Agassiz), *E. b. gutselli* (Hildebrand), and *E. b. pholidotum,* new subspecies.

***E. b. newmanii* has the highest scale counts, more dorsal rays, usually a fully scaled belly, and often a well-developed lip tip. The subspecies is found throughout the Tennessee River System (except in areas occupied by *gutselli*), the Cumberland River System, and west of the Mississippi River in the St. Francis, White, Arkansas, and Ouachita River systems. The population in the Tennessee River differs, on a racial level, from the populations of the Cumberland, St. Francis, Black, and upper White rivers. Another race of *newmanii* occurs in the Arkansas, Ouachita, Saline, and Little Red rivers.**

***E. b. gutselli* usually lacks opercle scales, has no upper lip tip, has low scale counts, and usually has a naked belly anteriorly. It intergrades with *newmanii* in the Hiawassee River System, but is allopatric with it in the Little Tennessee and Pigeon rivers. At present, *gutselli* is restricted to the headwaters of the Little Tennessee River and some tributaries of the Pigeon River.**

***E. b. blennioides* has higher scale counts than *pholidotum*; lower scale and dorsal-ray counts than *newmanii*; more lateral blotches and a higher incidence of a naked area on the belly than either. *E. b. blennioides* is distributed throughout the Ohio River drainage upstream from the Green River confluence, in the upper Genesee River in New York (Lake Ontario drainage), and in the Potomac River (Chesapeake Bay drainage).**

The new subspecies, *E. b. pholidotum,* has lower scale counts than *newmanii* and *blennioides,* and a small lip tip or none. All specimens examined had a completely scaled belly. Two races are recognized: the Wabash River–Great Lakes race and the Missouri race. The Missouri race is found in southern tributaries of the Missouri River (intergrading with *newmanii* in the Gasconade River), and in some Mississippi River tributaries south of the Missouri River confluence.

***E. b. newmanii* (Tennessee race) and *E. b. gutselli* seem to be the most primitive forms and appear to have had their origins in the southern Appalachian Mountains. *E. b. gutselli* may have had wider distribution in the past, possibly throughout the whole French Broad System. The Tennessee race of *newmanii* probably populated the Cumberland River System either by a downstream migration or by a headwater transfer. Movement across the Mississippi Embayment must have occurred in the**

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[1] Contribution No. 54, Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida 33149.

late Pliocene or early Pleistocene when the Mississippi, Ohio, and Tennessee rivers occupied separate channels with numerous connections.

E. b. blennioides **appears to have originated by transfer of** ***newmanii*** **stock from the headwaters of the Tennessee River into the Teays (New) River, where it evolved and later populated some of the downstream tributaries of the Teays.** ***E. b. blennioides*** **was able to move upstream into the Monongahela and lower Allegheny rivers and downstream in the Ohio River after the present courses of the two rivers were established by drainage changes during deglaciation. This subspecies reached the upper Genesee River from the Allegheny River via the Cuba glacial outlet in the post-Pleistocene. In the Genesee, the subspecies is now found only above Letchworth Falls. It entered the Potomac River System through stream piracy from either the Youghiogheny or upper Cheat River System.**

The Missouri race of ***E. b. pholidotum*** **probably evolved from an isolated population of** ***newmanii*** **in southeastern Missouri. Subsequently** ***pholidotum*** **moved up the Missouri River into the Osage River and across the Mississippi River into the Wabash River System. The Wabash–Great Lakes race used the Maumee outlet during Wisconsin deglaciation and spread into Michigan, the Lake St. Clair drainage of the Province of Ontario, and the southern tributaries of Lake Erie. During successive stages of lowering of the proglacial lake in the present Lake Erie and Lake Ontario basins, the Wabash–Great Lakes race spread into central New York, populating the lower Genesee River, the Seneca and Mohawk rivers, and the southwestern tributaries of Lake Ontario.**

INTRODUCTION

THE greenside darter, *Etheostoma blennioides* Rafinesque (1819), inhabits many streams of the Great Lakes, and Mississippi and Potomac river drainages. Differences have evolved among certain populations in these drainages. This paper describes the infraspecific variation and reviews the biology of this species.

The most extensive early account of *E. blennioides,* encompassing synonymy, description, and ecological information, was by Jordan and Evermann (1896b). Bean (1903), Forbes and Richardson (1920), and Evermann and Clark (1920) dealt with biology as well as taxonomy of the northern subspecies. More recently, Gerking (1945) described the distribution in Indiana, Fahy (1954) published on the life history of the northern subspecies, and Trautman (1957) discussed the two subspecies that occur in Ohio.

From an analysis of the species throughout its range, I recognize four subspecies: *E. b. blennioides* (upper Potomac, Genesee, and Ohio rivers); *E. b. newmanii* (Tennessee, Cumberland, St. Francis, White, Arkansas, and Ouchita rivers); *E. b. gutselli* (Little Tennessee and Pigeon rivers); and *E. b. pholidotum* n. ssp. (Great Lakes drainage, the Wabash and Mohawk rivers, and southern tributaries of the Missouri River).

MATERIALS

Study materials consisted of about 4000 specimens in 540 collections most of which were in the Cornell University Fish Collection (CU).

The following individuals and institutions lent me specimens and made their facilities available: Reeve M. Bailey, University of Michigan Museum of Zoology (UMMZ); James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); Herbert T. Boschung, Jr., University of Alabama; Frank B. Cross, Museum of Natural History, University of Kansas (KU); Shelby D. Gerking, Indiana University (IU); Robert H. Kanazawa, Ernest A. Lachner, Leonard P. Schultz, and W. Ralph Taylor, Division of Fishes, U. S. National Museum (USNM); Giles W. Mead, Museum of Comparative Zoology, Harvard University (MCZ); George A. Moore, Oklahoma State University (OAM); Robert D. Ross, Virginia Polytechnic Institute (VPI); Donald C. Scott, University of Georgia (UG); Philip W. Smith, Illinois Natural History Survey (INHS); Royal D. Suttkus, Tulane University (TU); Milton B. Trautman, Ohio State University (OSU);

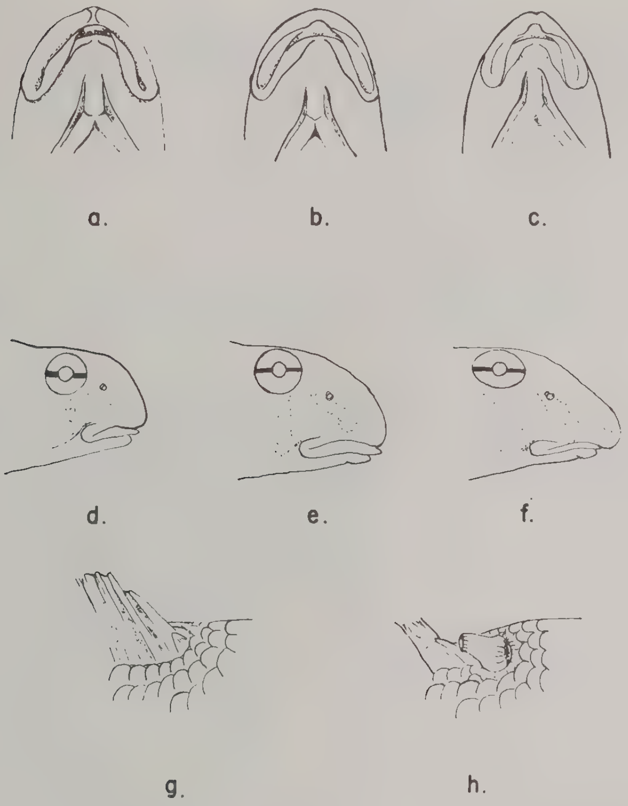

Fig. 1. Lip tip, snout shape, and genital papillae of *Etheostoma blennioides*. a, Tip absent or a slight bump on the anterior end of the upper lip (A). b, A distinct tip present but length shorter than lip width (S). c, Very distinct tip equal to or longer than lip width (L). d, Bluntly rounded snout (BR), not overhung (NO). e, Smoothly rounded snout (R). f, Elongated snout (LR), distinctly overhung (O). g, Genital papilla of breeding male, 80 mm SL. h, Genital papilla of breeding female, 65 mm SL.

and Arthur Witt, Jr., Museum of Zoology, University of Missouri (UM).

Methods

Characters Studied

Scale and fin-ray counts were made, by the methods of Hubbs and Lagler (1958:19–24) except for the transverse scale count, which follows Bailey (1959) who counted the scale rows from the origin of the second dorsal fin diagonally downward and posteriorly to, but not including, the mid-ventral scale row.

Scale counts.—The three counts were: lateral-line, transverse, and circumferential (least number of caudal peduncle scales). These counts reflect differences in scale size among the subspecies. Scale size, which was generally the same throughout a drainage or river system, proved to be the most useful character in defining subspecies.

Fin-ray counts.—Counts included the number of dorsal spines and soft rays, anal soft rays, and pectoral rays. All were of value in separating the subspecies.

Lip tip.—The small knob or tip at the end of the upper lip was classified by three grades of development (Fig. 1a–c): tip absent (A in tables); tip length shorter than lip width (S); tip longer than lip width (L).

Snout type.—The shape of the profile of the head from the eyes to the end of the snout occurred in three main types (Fig. 1d–f): bluntly rounded (BR in tables); smoothly rounded (R); and a longer, rounded snout (LR).

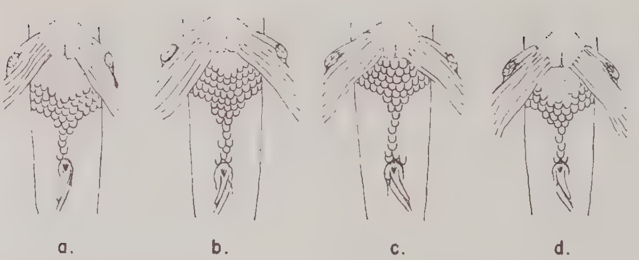

Fig. 2. Belly squamation in *Etheostoma blennioides.* a, Anterior part of belly with a large naked area (LNA). b, Anterior part of belly with a small naked area (SNA). c, Belly completely scaled (C). d, Belly fully scaled but anterior scales deeply imbedded (I).

Overhung snout.—A condition where the snout is large, gibbous, and in profile partly or completely obscures the tip on the upper lip (Fig. 1f). This characteristic is usually, but not always, correlated with the long snout shown in the figures. The condition is absent or present, and is abbreviated in the tables as NO (not overhung) and O (overhung).

Belly squamation.—Four categories of belly squamation are recognized (Fig. 2a–d): large triangular naked area at the anterior end of the belly, extending at least one-third the distance to the genital papilla (LNA in tables); small triangular naked area at the anterior part of the belly, extending less than one-third the distance to the genital papilla, but visible as a distinct naked patch (SNA); completely scaled belly up to the posterior interpelvic ridge (C); fully scaled belly but the anterior scales are deeply imbedded (I). The last type is essentially a type C squamation and does not occur often except in *E. b. blennioides,* which also has a high occurrence of types LNA, SNA, and C. The posterior scale rows, which were always present, are not illustrated in the figures.

Frenum.—A frenum is present in all subspecies. In *b. blennioides, b. newmanii,* and *b. pholidotum,* it is usually moderately to strongly crossed by the groove between the upper lip tip and the snout. In *b. gutselli,* and in a high percentage of *b. newmanii* × *gutselli* intergrades, the tip is reduced or absent and a frenum is distinctly visible.

Lateral blotches.—The number of lateral blotches differed among some subspecies. A blotch was counted as separate if it was distinct from blotches on either side of it. Among specimens that have "ditto mark" blotches (like the Arkansas River population of *E. b. newmanii*), both marks were recorded as a single blotch unless they had a gap between them equal to about twice the width of one mark.

Breast scales.—Counts of the number of breast scales revealed individual variation. The percentage of fish that had breast scales, however, varied between drainages.

Prevomerine teeth.—The occurrence of prevomerine teeth was determined throughout the range of the species. The percentage occurrence differed between *E. b. gutselli* and the other subspecies.

Measurements.—Measurements were not taken, except standard length. A preliminary study showed large random variation of body proportions.

Sources of Variation

The following sources of variation were considered to determine how they might affect conclusions based on meristic differences:

Asymmetric variation.—All bilateral structures were counted on the left side after a preliminary comparison of counts from both sides showed only random differences between sides.

Sexual variation.—The sexes were compared for differences in number of lateral-line scales and fin rays for all subspecies of *E. blennioides,* except *b. gutselli.* A chi-square test indicated no significant differences except for dorsal soft rays for *b. pholidotum* (chi-square, 4 df = 17.81, significant at the 1% level). Males had higher dorsal soft ray counts in *b. pholidotum* in all subsamples. Winn (1958a:174) indicated that *b. pholidotum* males sometimes were able to recognize other males by the form of the dorsal fin.

Year–class variation.—Comparisons were made of scale and fin-ray counts from three different years in *E. b. pholidotum* from Salmon Creek, New York. All chi-square values for the fin-ray data were nonsignificant, but year-to-year differences were significant for counts of lateral-line and transverse scales. The difference resulted from a high percentage of 58 lateral-line scales in one sample, and the occurrence of 57 and 59 scales (almost no specimens with 58 scales) in a later sample. Because sample means were so similar, they were also tested with Student's *t*, which showed no significant yearly differences for the two scale counts. The observed differences were adjudged to be the result of effects of environmental fluctuations on the year classes studied and to have no systematic significance (Moenkhaus, 1897). A more detailed discussion can be found in Miller (1964).

Development.—The smallest specimen studied, taken on 5 June (IU 113), measured 17.5 mm SL. The fins were completely developed but various areas were incompletely covered with scales. Squamation development proved significant, because specimens shorter than 30 mm SL may lack cheek and opercle scales. Below 25 mm, the lateral-line canal has not yet closed over, and scales may be missing along the upper sides. By about 30 mm, the fin rays are well-developed, all areas are scaled, and the lateral-line canal is completely covered. All specimens used in the meristic section of this study were over 30 mm SL.

Terminology

My use of the term "subspecies" is similar to that of Mayr, *et al.* (1953). I use "race" to denote a taxonomic group below the level of subspecies (as used by Raney, 1957), and "population" as defined by Marr (1957).

Diagnosis and Relationships

E. blennioides is distinguished from other species in the genus primarily by the fusion of the flesh over the anterior half of the maxillaries with the skin over the preorbitals (Hubbs and Lagler, 1958:104, fig. 45). Often the upper lip has a knob or tip, and the snout is bulbous and overhanging. Breeding males are bright green. Five–eight bright green bands on the sides may meet across the back or on the underside of the caudal peduncle. Orange to reddish-orange spots are scattered over the upper sides and dorsum.

In the present study, I have considered the relationships to *E. blennioides* of several closely related species in the subgenus *Etheostoma*. *E. gutselli* is only subspecifically distinct (a more detailed discussion is presented under subspecies accounts). *E. swannanoa* (Jordan and Evermann), *E. thalassinum* (Jordan and Brayton), and *E. inscriptum* (Jordan and Brayton) are a closely related species-group according to Richards (1966). *E. swannanoa* appears to be closely related to *blennioides* and probably derived from the same ancestral stock. Later, *swannanoa* probably gave rise to *thalassinum* and *inscriptum*. *E. rupestre* Gilbert and Swain and *E. zonale* (Cope) show marked similarities to *blennioides* but have several advanced characteristics (see below). Both species may have been derived from the early *blennioides* stock. I have not examined the relationships of all species in the subgenus, but three workers have recently presented pertinent information on the group.

In a table of vertebral counts, Bailey (*in* Bailey and Gosline, 1955) placed 15 species in the subgenus *Etheostoma* and apparently listed them in order of relationship; he placed *blennioides* and *gutselli* adjacent to each other and more or less separated from others in the subgenus.

More recently, Collette (1965) divided the subgenus into three species-groups on the basis of the presence and pattern of breeding tubercles. He placed *inscriptum, thalassinum, swannanoa, blennioides,* and *gutselli* in the *inscriptum* group, characterized by the presence of tubercles on the ventral scales of males. His other two groups were the *variatum* group (with tubercles on the ventral scales in both sexes), and the *zonale* group (nontuberculate).

Richards (1966) divided the subgenus mainly on differences in the prevomerine and palatine dentition and concluded that the subgenus included three groups. The primitive *variatum* group, which has both palatine and prevomerine teeth, includes *variatum* Kirtland, *tetrazonum* (Hubbs and Black), *euzonum* (Hubbs and Black), *osburni* (Hubbs and Trautman), and *kanawhae* (Raney). An intermediate group of *thalassinum, inscriptum,* and *swannanoa* has reduced palatine and prevomerine dentition (palatine teeth absent in some populations).

The species of the most specialized group, *blennioides, zonale, rupestre,* and *histrio* Jordan and Gilbert, lack palatine teeth and have only reduced numbers of prevomerine teeth.

I agree that the *variatum* group is a natural one. I do not entirely agree with the other species-groups of Collette or Richards. In my analysis, *E. blennioides* and *E. gutselli* are only subspecifically distinct, but the occurrence of prevomerine teeth (a prime character of Richards) is highly variable within the species (more frequently present in *E. b. gutselli* than in the other subspecies), and *gutselli* has a well-developed frenum (as do *thalassinum, inscriptum,* and *swannanoa*). Reliance on these characters alone would imply that *E. b. gutselli* is most closely related to the *inscriptum* group. However, *gutselli* has distinctly fewer scales than other subspecies of *blennioides,* and has lost scales on the opercle and anterior part of the belly; thus on the degree of squamation, *E. b. gutselli* exhibits more advanced characteristics than other subspecies of *E. blennioides.* Prevomerine teeth or squamation used alone, therefore, may not be reliable characters for judging relations.

Color patterns indicate close relationships between species placed in separate groups on the basis of tubercle patterns by Collette. Both *zonale* and *rupestre* are basically green; green body bars in *zonale* are similar to *blennioides. E. rupestre* has orange-brown spots on the sides and dorsum (bright orange in *blennioides*); *zonale* and *rupestre* (and *E. swannanoa*) have an orange basal band in the first dorsal fin as in *blennioides,* but both *zonale* and *rupestre* have only six dorsal blotches (possibly an advanced condition from the seven in *blennioides*). Further, *zonale* frequently has only five branchiostegals, which may also represent an advanced condition from the invariable six in *blennioides* (and in *rupestre*).

On the other hand, the presence of the fleshy bridge connecting the maxillaries to the preorbital separates *blennioides* from all others in the subgenus; vertebral counts also distinguish *blennioides* to a high degree. Although the tubercle pattern in *blennioides* is similar to that in the *inscriptum* group, and palatine and prevomerine dentition are similar to the *zonale* group, I hold that in themselves these or other individual characters are not necessarily reliable indicators of relationships.

When all the characteristics of *blennioides* are considered (including its wide distribution and adaptation to varied environments), *blennioides* appears intermediate in the evolutionary sequence of the subgenus. I believe the center of speciation was in the Appalachian highlands and that a more generalized ancestor (or *variatum* type) gave rise to both *blennioides* and *swannanoa.* The latter split off populations that evolved into *thalassinum* and *inscriptum,* and the original *blennioides* stock split off populations that gave rise to *rupestre* and *zonale.*

SUMMARY OF BIOLOGY

Sexual Dimorphism

Sexual differences are marked in spawning coloration, development of breeding tubercles, size of the genital papilla, growth rate, and body size. The first three are related to the maturation of the gonads as the spawning season approaches. Fahy (1954: 167) delineated the breeding season for New York populations of *blennioides* [= *E. b. pholidotum*] as approximately the second week in April through the second week in June, reaching a peak in May. Throughout the range of the species, the spawning period coincides with warming of water to temperatures in the low 50's (°F). Spawning begins at 53°–55° F.

Winn (1958a:172) recorded slightly larger anal, first dorsal, pectoral, and pelvic fins in males than in females of Michigan *blennioides* [= *E. b. pholidotum*]. Lachner *et al.* (1950:96) reported similar findings but found smaller pectorals in males than in females and stated that the pelvic fins were the same in both sexes of *E. b. blennioides.* The fact that these authors studied different subspecies may account for the differences in their findings. Although I found no sexual dimorphism in the number of pectoral rays, I did not make measurements of the length of the pectoral fin.

During the breeding season, the flesh covering the tips of the pelvic spines of males becomes a swollen, flattened pad, as do the fleshy tips of the soft rays, though to a lesser extent. In both sexes, the ventral edge of the pectorals is slightly thickened during the spawning period. The tips of the anal rays of large breeding males often become thickened. After spawning, these swellings decrease markedly but begin to appear again in the fall.

Spawning coloration.—Color pattern of fresh specimens in various stages of sexual development was studied extensively in the spring of 1962, when samples from most of the major drainage systems were examined. The considerable differences found in the degree of color development reflect variations in local spawning time, but the basic color pattern appeared similar throughout the range of the species. Fahy (1954:141–143) described in detail both breeding and nonbreeding coloration of fish in New York populations [= *pholidotum*], as did Trautman (1957:572) for Ohio populations [= *pholidotum* and *blennioides*]. The following paragraphs describe major differences between color patterns of the sexes.

Melanism increases markedly in males, beginning in late fall; by January the breast is covered with melanophores. In late winter the head and body darken, and by spawning time most of the head blotches may be obscured. Head and body blotches in the female also darken just before the breeding season. At spawning, the males develop dark green bands on the body which obscure the usual lateral U-shaped blotches. Parts of the pectoral, pelvic, anal, and caudal fins turn brilliant green (Jordan and Evermann, 1896b:1052), as do other parts of the body. Some specimens develop a bluish cast at the base of the pectoral fins, on the breast, and on the anterior part of the belly. The spinous dorsal fin is typically banded, with a red-orange basal band, a narrow light-green median band, and an intense green outer band. The second dorsal fin has an orange to reddish-brown basal area, wider anteriorly; a moderately dark green band separates this strip from an outer light band, usually yellow to yellow-green. A thin reddish-brown band is sometimes evident at the base of the anal fin; this feature is not seen on many brightly colored specimens—it may appear just as spawning is about to start, and fade soon after. Near spawning time, the scattered red-orange spots that cover one to several scales on the dorsum and sides become prominent in both sexes, but are sometimes obscured on females because of darkening of the lateral blotches.

Breeding females tend to develop a body color predominantly yellow to yellow-green. The caudal fin is usually yellowish and a yellow band appears on the anal and dorsal fins.

E. b. gutselli and *E. b. blennioides* display more lateral blotches (usually eight or nine) than the other two subspecies. The fins in *b. gutselli* often have more irregular blotches than other subspecies.

The orange spots on *E. b. blennioides* from certain localities are sometimes indistinct. The subspecies usually has the typical orange spotting on the dorsum.

Breeding tubercles.—Throughout the range of the species, tubercles often were found only on adult males taken at or near the height of the breeding season. The time of tubercle development varies with locality; it has been observed as early as 26 March on specimens from the Licking River System, Kentucky (CU 37520) and as late as 26 May in the Thames River, Ontario (UMMZ 85545). In a given locality, the tubercles appear to be ephemeral and are probably well-developed only at actual spawning time.

The tubercle develops as a marked thickening and elongation into a point on the posterior edge of a scale. Tubercles begin on the belly, about a third of the way between the posterior interpelvic ridge and the anus, and extend posteriorly to the base of the caudal fin; they occur on three scale rows anteriorly and four or five rows on the sides near the genital papilla. Tuberculate scale rows decrease to three opposite the genital papilla, and tubercles extend posteriorly on two scale rows on each side above the anal fin. Posterior to the anal fin, tubercles are more irregular but are present on four scale rows on the ventral part of the caudal peduncle. Tuberculate scales terminate in two rows on either side of the fleshy covering of the ventral rudimentary caudal rays. No tubercles have been found on the fins. Specimens of *E. b. gutselli* from late spring collections are scarce, but two adult males (UG uncat.) taken on 9 May 1959 evidenced tubercle development. The pattern was similar to that of specimens from other areas but the tubercles lacked the pointed posterior edge. The tubercle pattern does not vary geographically.

Genital papillae.—In males, the size is fairly uniform throughout the year, but the papilla darkens as the breeding season approaches (Fig. 1g). In females, the papilla

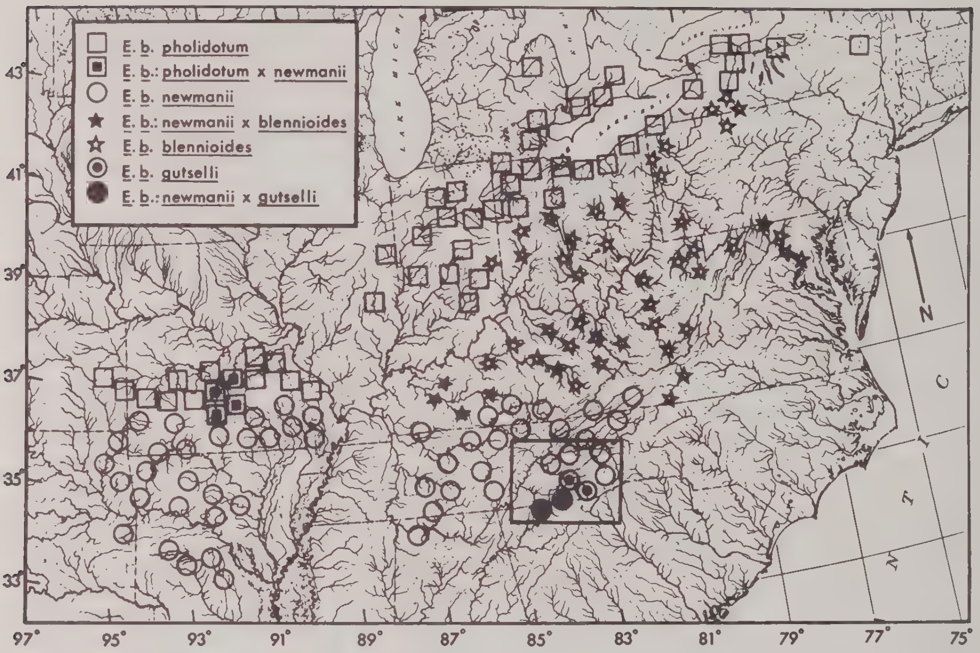

Fig. 3. Distribution of the subspecies of *Etheostoma blennioides* and intergrade populations of *E. b.*: *pholidotum* × *newmanii* (Gasconade River), *E. b.* : *newmanii* × *blennioides* (Green River), and *E. b.* : *newmanii* × *gutselli* (Hiawassee River). Symbols are located on areas where collections have been taken but do not represent the actual number of collections examined. The distribution of *E. b. gutselli*, *E. b. newmanii* (in part), and *E. b.* : *newmanii* × *gutselli* intergrades (inset area) are plotted in detail in Fig. 4.

lengthens and swells in January or February and small dark patches appear on some specimens (Fig. 1h). After spawning it shrinks rapidly to almost the same size as the male papilla.

Growth rate and body size.—Males were larger than females in almost all collections that contained adult fish, and both Fahy (1954:193) and Lachner *et al.* (1950:105–106) showed that males grow faster and larger. The difference in size of the sexes is statistically significant at the end of the first summer and increases each year thereafter. At maximum size, males were six–eight mm longer than females.

Sex ratio.—Lachner *et al.* (1950:97), found a sex ratio of males to females significantly greater than 1:1 in all age groups in all collections of *E. b. blennioides* from a tributary of the Allegheny River. Fahy (1954:154–156) showed that essentially a 1:1 ratio existed in collections from a tributary of Lake Ontario [= *E. b. pholidotum*]. This difference may be subspecific, but it may also be due to differences in sampling methods. Fahy often found juveniles and females in quiet water (pools above or below a riffle), whereas Lachner *et al.* apparently collected exclusively from large riffles of a large stream.

Habitat and Ecology

The subspecies of *E. blennioides* can be found in all types of habitat from clear, cold mountain streams to relatively quiet lake shores (Fig. 3). The species prefers rivers or streams of moderate to fast current and low turbidity, with a substrate of large gravel to rocks. It may or may not be in association with green algae—indeed, it is collected as often as not on bare substrate (Schwartz, 1965)—but it remains to be seen whether this species, if presented with a choice of riffle areas with or without algae, would not select the area with algae, particularly during spawning.

E. b. gutselli is found primarily in clear, mountain streams, usually in association with fast-water species like *Rhinichthys cataractae*

(Valenciennes), *Hypentelium nigricans* (LeSueur), and *Cottus bairdii* Girard. It has been taken in the same stream with numerous other species as well, but on these occasions the habitat was usually a quiet pool or backwater. Lennon (1962) who listed 72 species from the Great Smoky Mountains National Park, took *E. b. newmanii* in the lower courses of large streams and *E. b. gutselli* in the Tuckesegee River. Hiawassee River intergrades (*gutselli* × *newmanii*) were also taken with numerous other species. An anomaly in distribution was the absence of *E. rufilineatum* from the Little Tennessee System upriver from the Abrams Creek confluence, but the species was common in the Hiawassee System.

The other subspecies of *E. blennioides* can generally be found with almost any fishes that inhabit riffles, or near those that live close to or in pools or backwaters, in moderate-sized to large streams. Many species of minnows, darters, and suckers have been taken in association with *E. blennioides,* depending upon locality and water conditions at the time of capture.

E. blennioides was present in every stream system of Ohio, at least as strays, according to the 1920–50 survey (Trautman, 1957:572–573, map 157). The largest populations were in the streams along the Allegheny Front Escarpment, the streams of moderate to high gradients of southwestern and west central Ohio [= *E. b. blennioides*], and around the Lake Erie Islands [= *E. b. pholidotum*]. These three areas represent a tremendous variation in habitat, from high-gradient streams to lake shores. Trautman stated that a decrease in abundance in parts of the Maumee and Auglaize rivers after 1930 followed an increase in turbidity of the water. He found *E. b. blennioides* absent (except for isolated populations or strays) in the mature, base-level, or low gradient, unglaciated streams of southeastern Ohio between the line of glaciation and the short, direct tributaries of the Ohio River. The subspecies was rare in the Ohio River proper during the survey, but Trautman believed it must have been a permanent resident there before impoundment, elimination of riffles, and the increase in siltation.

Trautman (1957) discussed different habitat preference for the two subspecies of *E. blennioides* in Ohio. His "prairie type" [= *E. b. pholidotum*] was associated with various aquatic plants, including several rooted aquatics as well as algae and mosses. The "Allegheny type" [= *E. b. blennioides*] was associated only with algae and mosses, but Lachner *et al.* (1950) found many kinds of plants, including *Potamogeton* and *Vallisneria,* in a riffle area of an Allegheny River tributary that yielded large numbers of *E. b. blennioides.* Gerking (1945:13) listed *E. blennioides* [= both *b. pholidotum* and *b. blennioides*] as most common in riffles of smaller streams that had a substrate of small to large stones, a swift current, and predominantly algal vegetation. Schwartz (1965), however, did not believe that *E. blennioides* actually preferred a vegetated habitat, and cited numerous collections from bare substrates in New York, Pennsylvania, West Virginia, Virginia, and Maryland.

Habitat preferences of northern populations [= *E. b. pholidotum*] have been described by several authors, including Bean (1903:513), Forbes and Richardson (1920:293–294), Gerking (1945:13), and Hubbs and Lagler (1958:109). These authors generally hold that the northern greenside darter lives in fast, clear streams and prefers riffles containing green algae. Fahy (1954:144–146) and Winn (1958a:161) cited the occurrence of certain age groups or assemblages of females in pools or quiet water areas in the streams they investigated. Several collections that I examined came from lake shores or large rivers, as well as from the usual fast-water streams. *E. b. pholidotum* within its range probably occupies most habitats that are not overly turbid or polluted. In spawning season, the fish apparently seeks out riffles or moving water.

Reproductive Behavior

The reproductive behavior of northern populations [= *E. b. pholidotum*] was treated extensively by Fahy (1954) and Winn (1957, 1958a, 1958b). This subspecies commonly winters downstream and migrates upstream to the riffle areas to spawn, from April through May. According to Winn (1958b:200), the males hold territories (aquarium experiments), but Fahy (1954) saw no territoriality among *blennioides* breeding in hatchery troughs. The female, with the male following, moved into algae to spawn and assumed a position (on the algae) that varied from near horizontal to almost 90°, whereupon the male mounted in the usual darter fashion (Winn, 1958a:177, fig. 1). The two fish then vibrated in unison for several seconds, at which time the eggs were extruded. A pair may spawn more than once, at short time intervals. Presence of algae is probably not a requisite for spawning—Schwartz (1965) observed *E. b. blennioides* spawning over sand.

Etheostoma blennioides newmanii (Agassiz)

Hyostoma newmanii Agassiz, 1854:305 (original description, Ala., near Huntsville).

Hyostoma newmanii. Jordan and Gilbert, 1877:90; Hubbs and Greene, 1928:385 (synonym of *E. blennioides*).

Hyostoma cymatogrammum. Cope, 1865:82 (synonym of *Pileoma cymatogramma* Abbott); Cope, 1870a:270 (headwaters of Cumberland, Tennessee, and French Broad rivers); Cope, 1870b:450 (French Broad River).

Hyostoma blennioperca Cope, 1869:215 (original description, tributaries of Kanawha and Holston rivers, Va.; type-series: ANSP 14004, 14006–8, 14020–25, 14026–35); Cope, 1870a:270 (variation of *H. cymatogrammum*); Fowler, 1907a:522 (synonym of *Diplesion blennioides*; largest specimen from Holston R. collection selected as lectotype = ANSP 14026).

Diplesium blennioides. Jordan, 1876:224 (Holston R.); Jordan and Brayton, 1878: 58, 73 (upper Tennessee and Cumberland rivers); Jordan and Gilbert, 1882:497 (synonymy, range, color pattern, description); Jordan and Swain, 1883:249 (Clear Fork, Cumberland R.).

Diplesium newmani. Jordan, 1877a:15 (Tennessee R.); Jordan, 1878a:439 (Tennessee R.).

Etheostoma blennioides. Cope, 1870a:262 (Cumberland R.); Cope, 1870b:493 (Cumberland R.); Jordan, 1890:148, 153 (Holston R. and French Broad R.); Gilbert, 1891:150 (Cypress, Shoal, and Big Nance creeks, Ala.); Meek, 1891:128, 130, 135, 137, 141 (upper Arkansas R., White, Little Red, Black, and Ouachita rivers); Woolman, 1892:267–268 (Cumberland R.); Kirsch, 1893:260–264, 266–268 (tributaries of Cumberland R.); Evermann and Kendall, 1895:471 (Indian Creek of Arkansas R.); Jordan, 1899:125 (distribution and synonymy, in part); Fowler, 1923:13, 18, 24 (Holston, French Broad, Cumberland rivers); Jordan, 1929:158 (synonymy, description, and range, in part); Fowler, 1945:84 (synonymy in range records); Moore and Paden, 1950:90 (Illinois R. of Arkansas R. in Okla., habitat); Hall, 1952: 58 (upper Arkansas R.); Moore, 1952:10; Cross and Moore, 1952:409 (Poteau R. of Arkansas R. in Okla.); Hall, 1953:37 (Tenkiller Reservoir, Arkansas R. in Okla.); Lennon, 1954:5 (upper Little Pigeon R., Great Smoky Mountains National Park); Bailey and Gosline, 1955:16 (number of vertebrae); Lennon and Parker, 1959:15 (Abrams Creek, Great Smoky Mountains National Park); Lennon, 1962:6 (lower courses of large streams of Great Smoky Mountains National Park); Ross and Carico, 1963:17, 20–21 (Holston R.).

Diplesion blennioides. Kirsch, 1892:290 (Cumberland R.); Bean, 1903:512–513 (N. Y. but gives counts for *E. b. newmanii*); Jordan, 1905, 1:247, fig. 176 (Clinch R.), 2:312, fig. 246 (description, range in part); Fowler 1907a:522 (synonymy, range, and records); Smith, 1907:259–260 (synonymy, description, range, distribution; N. C.); Evermann and Hildebrand, 1916:450 (records from Tennessee R.); Evermann, 1918: 357 (records from Ky. and Tenn., list of records).

Pileoma cymatogramma. Fowler, 1907a:522 (synonymy of *Diplesion blennioides*).

Etheostoma blennioides newmanii. Kuhne, 1939:93 (subspecies *newmanii* recognized); Black, 1939:154, map 55 (distribution in Ark. and of southern form, in part, habitat).

Etheostoma blennioides newmani. Raney, 1952:97 (as species associate of *Ichthyomyzon hubbsi* in Nottely R., Ga.); Miller, 1965:1234 (diss. abstr.).

Misidentifications: *Etheostoma blennioides.* Fowler, 1945:355–356 (upper Coosa R. = *Etheostoma* (*Ulocentra*) sp.); Boschung, 1961:280 (listed Fowler's 1945 records from Coosa R.).

Types.—*Hyostoma newmanii,* USNM 1865 (male, 93 mm SL) selected as lectotype *in* Collette and Knapp (1967:53), Ala., near Huntsville (Tennessee R. drainage); Newman. The counts for the lectotype are: lateral-line scales 71; transverse scales 20; least caudal peduncle scales 29; A.II, 7; D.XIV-12; P_1, 15-15; cheeks, opercles, and belly completely scaled.

TABLE 1. A COMPARISON OF FOUR SUBSPECIES OF *Etheostoma blennioides.* Ranges given under name of each subspecies. (All numbers are means.)

Character	*E. b. pholidotum* Missouri, Wabash-Great Lakes races	*E. b. blennioides* Upper Ohio, Potomac, Upper Genesee	*E. b. newmanii* Tennessee, Cumberland drainages	*E. b. gutselli* Upper L. Tennessee + Upper Pigeon
Lateral-line Scales	61.85 Mo. 58.61 Wab.-Gr. L.	65.42	77.38 Cumb. 70.69 Tenn.	56.79
Transverse Scales	16.36 Mo. 15.17 Wab.-Gr. L.	17.74	21.65 Cumb. 19.38 Tenn.	16.56
Least Caudal Ped. Scales	21.87 Mo. 21.10 Wab.-Gr. L.	23.32	28.71 Cumb. 26.32 Tenn.	21.77
Anal Soft Rays	7.95 Mo. 8.44 Wab.-Gr. L.	8.01	8.05 Cumb. 8.09 Tenn.	7.88
Dorsal Spines	12.88 Mo. 12.91 Wab.-Gr. L.	13.02	13.49 Cumb. 13.85 Tenn.	12.75
Dorsal Soft Rays	12.86 Mo. 13.04 Wab.-Gr. L.	12.89	13.11 Cumb. 13.38 Tenn.	14.08
Left Pectoral Rays	14.84 Mo. 14.58 Wab.-Gr. L.	14.56	14.83 Cumb. 14.82 Tenn.	15.01
Lateral Blotches	7.11 Mo. 7.44 Wab.-Gr. L.	7.68	7.29 Cumb. 7.25 Tenn.	8.43
Lip Tip, mode	Absent or short tip	Short tip	Long tip	None; distinct frenum
Belly Squamation, mode	Completely scaled	Small naked area or completely scaled	Completely scaled	Large and small naked area
Snout Type, mode	Bluntly rounded	Bluntly rounded or rounded	Long-rounded (Cumb.) Rounded (Tenn.)	Long-rounded
Overhung Snout	Rarely	Rarely	Usually (Cumb.) Sometimes (Tenn.)	Never
Opercles	Scaled	Scaled	Scaled	Usually naked
Head Shape	Narrow, snout not swollen	Narrow, snout not swollen	Flattened, snout swollen, cheeks bulged (Cumb. dr.); narrow, snout normal (Tenn. dr.)	Narrow, snout long, not swollen
Prevomerine Teeth (% occurrence)	< 10%	< 10%	< 10%	47%

Diagnosis.—*E. b. newmanii* differs from the other subspecies in having very high scale counts, more dorsal spines and rays, and (most specimens) a well-developed lip tip (Fig. 1c, Table 1).

Distribution and relationships.—*E. b. newmanii* occurs throughout the Tennessee River System (except possibly some of the tributaries entering from the west in western Tennessee and Kentucky), in the Cumberland River System, and west of the Mississippi River in the St. Francis, White, Arkansas, and Ouachita river systems (Fig. 3).

East of the Mississippi River, *E. b. newmanii* has differentiated into two races—the Tennessee River race and the Cumberland River race. The Tennessee race occurs in most of the Tennessee River and its tributaries except the upper Little Tennessee and Pigeon rivers (occupied by *E. b. gutselli*), the Hiawassee River (occupied by *newmanii* × *gutselli* intergrades), and the lowland areas between the lower Tennessee River and the Mississippi River in western Tennessee and Kentucky. The Cumberland race occurs throughout the Cumberland River System

TABLE 2. LATERAL LINE SCALE COUNTS FOR MAJOR POPULATIONS OF *Etheostoma blennioides.*

Subspecies and River	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	N	x̄
E. b. gutselli	1	–	–	6	9	7	19	12	8	15	5	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	86	56.79
E. b. :gutselli × newmanii	–	–	–	–	–	–	5	2	5	5	11	16	10	19	9	8	5	4	–	2	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	103	62.18
upper Hiawassee R.	–	–	–	–	–	–	–	–	–	1	4	7	4	9	9	5	4	4	–	2	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	51	63.80
Toccoa R.	–	–	–	–	–	–	5	2	5	4	7	9	6	10	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	52	60.60
E. b. newmanii	–	–	–	–	–	–	–	–	–	1	1	4	7	12	20	38	39	65	104	100	119	144	151	125	126	94	99	82	83	60	60	29	33	18	11	3	2	1,630	72.93
Tennessee R.	–	–	–	–	–	–	–	–	–	1	1	–	2	4	5	20	16	23	49	42	54	64	51	42	37	26	10	7	7	1	1	2	1	–	–	–	–	466	70.69
Holston R.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	2	11	13	19	14	17	15	7	9	3	3	3	1	1	–	1	–	–	–	–	122	71.65
Powell R.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	4	–	3	7	2	3	5	1	2	–	–	–	–	–	–	–	–	–	–	–	–	28	69.57
Clinch R.	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	4	5	7	10	7	7	5	4	6	2	1	–	1	1	–	–	–	–	–	–	–	–	64	69.14
upper French Broad R.	–	–	–	–	–	–	–	–	–	1	–	–	1	–	1	8	–	3	3	1	5	4	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	28	67.39
Pigeon R., L. Pigeon R.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3	5	4	9	4	2	18	10	6	4	3	1	1	–	–	–	1	–	–	–	–	–	72	70.50
Little R.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	3	6	5	2	3	5	5	5	5	–	2	–	–	–	–	–	–	–	–	43	72.09
lower Tennessee R.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	2	2	7	10	4	14	18	12	9	16	8	1	2	1	–	–	1	–	–	–	–	–	109	71.22
Cumberland R.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	3	3	6	8	15	13	16	18	29	30	31	33	30	21	20	13	9	2	–	303	77.38
S. Fork and upstream	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	3	3	3	6	11	12	3	7	8	9	7	6	–	2	–	1	–	–	–	84	74.12
downstream	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	2	4	1	13	11	21	20	25	24	30	19	20	12	9	1	–	215	78.60
St. Francis R.	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	2	4	3	3	6	11	9	7	9	13	2	2	2	–	–	–	–	–	–	–	–	–	74	71.11
Current-Black R.	–	–	–	–	–	–	–	–	–	–	–	2	2	1	4	2	3	15	10	12	9	17	27	12	12	5	4	–	–	–	–	–	–	–	–	–	–	137	70.29
upper White R.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	4	1	6	13	16	18	20	25	8	19	2	6	4	1	1	1	149	77.05
L. Red R.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	4	4	5	6	10	5	13	9	8	11	4	3	4	1	1	–	1	92	76.08
Arkansas R.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	3	9	8	14	18	28	25	20	18	22	13	11	6	6	1	2	–	–	–	–	207	73.53
Ouachita R.	–	–	–	–	–	–	–	–	–	–	–	–	–	1	6	4	5	12	18	13	13	19	14	11	5	4	1	1	1	1	–	–	–	–	–	–	–	129	69.86
Saline R.	–	–	–	–	–	–	–	–	–	–	–	1	3	6	5	8	7	8	9	3	6	1	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	60	66.48
E. b. :newmanii × blennioides																																							
Green R.	–	–	–	–	–	–	–	–	–	–	–	1	5	6	9	14	18	17	28	14	20	13	10	9	1	1	1	1	1	1	–	–	–	–	–	–	–	170	68.18
E. b. blennioides	–	–	–	–	–	–	2	6	9	15	38	32	76	91	118	115	108	114	82	71	31	24	18	9	5	2	1	1	2	–	–	–	–	–	–	–	–	970	65.42
Ohio R.																																							
Salt R.-Harrod's Cr.	–	–	–	–	–	–	–	–	–	1	2	2	9	1	4	11	7	5	4	–	2	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	49	64.80
Kentucky R.	–	–	–	–	–	–	–	–	–	–	–	–	1	7	10	11	9	9	16	19	12	9	4	3	2	2	–	–	–	–	–	–	–	–	–	–	–	114	67.88
S. Fork–upstream	–	–	–	–	–	–	–	–	–	–	–	–	1	4	3	4	2	1	6	7	2	6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	37	67.41
downstream	–	–	–	–	–	–	–	–	–	–	–	–	–	3	7	7	7	8	9	11	10	3	3	3	2	2	–	–	–	–	–	–	–	–	–	–	–	75	68.09
Whitewater R.-Miami R.	–	–	–	–	–	–	–	–	–	–	1	–	3	8	7	7	5	9	4	2	1	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	50	65.62
Licking R. (Ky.)	–	–	–	–	–	–	–	–	–	–	1	–	2	1	5	3	3	5	5	6	2	3	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	38	67.13

TABLE 2. *Continued.*

Subspecies and River	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	N	x̄
E. b. blennioides (continued)																																							
Ohio R. (continued)																																							
Scioto R.	–	–	–	–	–	–	–	–	–	–	2	3	8	9	14	13	6	19	8	9	5	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	98	65.66
Tygerts Cr. to Guyandot R.	–	–	–	–	–	–	–	–	–	1	–	1	2	1	5	2	3	5	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	65.42
Big Sandy R.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	7	2	3	1	3	2	6	4	3	–	1	–	2	–	–	–	–	–	–	–	–	35	70.31
Kanawha R.	–	–	–	–	–	–	–	5	4	9	14	7	17	24	25	17	15	16	6	6	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	167	63.53
upper	–	–	–	–	–	–	–	4	14	9	12	4	14	19	21	10	6	7	5	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	117	62.89
lower	–	–	–	–	–	–	–	1	–	–	2	3	3	5	4	7	9	9	1	5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	50	65.04
L. Kanawha, Big Wheeling Cr.	–	–	–	–	–	–	–	–	2	1	5	3	4	8	5	5	4	3	1	2	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	45	63.73
Muskingum R.	–	–	–	–	–	–	2	–	2	2	6	11	4	7	11	8	8	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	66	62.98
Monongahela R.	–	–	–	–	–	–	–	–	1	–	–	3	5	12	10	12	13	11	9	4	1	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	85	65.48
Allegheny R.	–	–	–	–	–	–	–	1	–	1	4	2	11	6	9	9	8	13	7	6	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	82	65.15
upper Genesee R.	–	–	–	–	–	–	–	–	–	–	2	–	2	4	4	10	8	9	8	5	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	53	65.91
Potomac R.	–	–	–	–	–	–	–	–	–	–	–	–	6	3	6	6	11	5	4	6	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	50	65.90
E. b. newmanii × *pholidotum*																																							
Gasconade R.	–	–	–	–	–	–	–	–	1	2	–	4	2	6	9	9	1	5	5	3	1	4	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	53	65.25
E. b. pholidotum	–	3	3	11	29	41	66	116	128	124	134	92	89	57	52	26	14	9	12	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1,009	59.56
Missouri race	–	–	–	1	2	3	5	9	19	22	38	37	42	28	37	16	13	7	12	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	294	61.85
Osage R.	–	–	–	1	2	3	5	8	16	15	18	23	20	13	18	5	4	2	3	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	157	60.94
Eastern Mo. group	–	–	–	–	–	–	–	1	3	7	20	14	22	15	19	11	9	5	9	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	137	62.90
Wabash-Gr. Lakes race	–	3	3	10	27	38	61	107	109	102	96	55	47	29	15	10	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	715	58.61
Wabash R.	–	–	–	–	2	2	6	14	23	26	37	18	23	15	11	7	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	186	60.22
Maumee R.	–	–	–	1	1	3	7	12	14	16	15	11	11	7	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	101	59.35
Michigan	–	–	–	–	4	1	5	12	15	12	13	6	4	3	3	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	80	59.00
Lake St. Clair	–	1	–	1	1	4	8	9	12	5	8	4	2	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	57	58.00
Lake Erie	–	1	1	1	6	8	11	16	25	16	10	6	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	104	57.65
Lake Ontario	–	–	–	1	2	10	13	31	11	22	13	9	6	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	119	58.03
lower Genesee R.	–	–	–	4	6	10	7	9	7	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	48	56.08
Seneca R.-Mohawk R.	–	1	2	2	5	–	4	4	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	54.95

and appears most closely related to several populations west of the Mississippi River.

Fowler (1945:355–356) listed seven collections of *blennioides* from the Coosa River System of northeastern Alabama (ANSP 79880–79886), but upon examination I found these to be *Etheostoma* (*Ulocentra*) sp. Boschung (1961:280) did not report *blennioides* (except Fowler's records) in his study of the fishes of the Coosa River System.

Scale counts of fish from the upper French Broad River differed slightly from those of specimens found in the rest of the Tennessee drainage, but the difference was not enough to distinguish the upper French Broad population from the Tennessee race (Tables 2–4).

The Cumberland race of *E. b. newmanii* differs from the Tennessee race most significantly in having higher scale counts (Tables 2–4) and an overhung snout in 90% of the specimens examined (Table 9). The head shape of most specimens of the Cumberland race differs slightly from most of the Tennessee River race—the head is flattened, the cheeks and opercles bulge, and the flesh above the upper lip is swollen (which accounts for the high occurrence of the overhung snout). Although other characters and counts are in frequencies similar to those of the Tennessee race, the Cumberland population is considered a separate race on the basis of the higher scale counts and differences in head shape. Some differences occur in meristic characters between upper and lower Cumberland specimens—upper Cumberland specimens have lower scale counts, a higher proportion of short (S) or no (A) lip tip, a higher proportion of large (LNA) and small (SNA) naked area types of belly squamation, and more lateral blotches—particularly upstream from the vicinity of the South Fork (Tables 2–4, 8). The differences are not clinal. Comparison with the Kentucky River data shows that the upper Cumberland River specimens are similar to the Kentucky River population of *E. b. blennioides* in the above characters, but lip tip development and numbers of lateral blotches for the upper Kentucky form are similar to those for the lower Cumberland form. Apparently a two-way transfer of *E. b. blennioides* and *E. b. newmanii* occurred between the Kentucky and Cumberland rivers as the result of a stream capture, well-documented by Kuehne and Bailey (1961). This stream capture and subsequent transfer is mentioned later (under *E. b. blennioides*), with evidence indicating that the Kentucky River population (*E. b. blennioides*) was not influenced to as great an extent as was the upper Cumberland population (*E. b. newmanii*) by the exchange.

West of the Mississippi River, *E. b. newmanii* occurs in the Whitewater, Castor, and St. Francis rivers, the White River System from the Little Red River upstream, the Arkansas River System, and the Ouachita River System.

Only 13 specimens were available from the Whitewater River in southeastern Missouri. The scale counts, which were somewhat lower than those in the St. Francis River population but higher than those in the Meramec River population, are included, with other meristic data, under the St. Francis.

In the White River System, the Little Red River population differs from both the Current-Black population and the upper White population upstream of the Black-White confluence (Tables 2–9). The St. Francis and Current-Black populations are similar in almost all counts but have lower scale counts than specimens from the upper White (Tables 2–4). All three populations have the characteristic head and snout shape of the Cumberland race. On the basis of head form (Table 9) and similarity of meristic data other than scale counts, the St. Francis, Current-Black, and upper White populations are assigned to the Cumberland race. On the basis of lower scale counts, the St. Francis and Current-Black populations differ from the upper White River population.

The Arkansas, Ouachita, and Saline river populations differ from the St. Francis and the White river populations (except that of the Little Red River) in almost all meristic characters (Tables 2–9), and in head shape, they usually lack the flattened appearance, the bulging cheeks, and swollen snout. The Arkansas, Ouachita, and Saline river populations vary clinally: scale counts for the Arkansas and Saline rivers are decidedly different and those of the Ouachita generally are intermediate (Tables 2–4). Because of the general similarity of head and snout shape and the gradation of differences in scale counts, the Arkansas, Ouachita, and Saline

TABLE 3. TRANSVERSE SCALE COUNTS FOR MAJOR POPULATIONS OF *Etheostoma blennioides*.

Subspecies and River	13	14	15	16	17	18	19	20	21	22	23	24	25	N	x̄
E. b. gutselli	–	2	10	25	37	11	1	–	–	–	–	–	–	86	16.56
E. b. :gutselli × newmanii															
Hiawassee R.	–	–	4	29	32	29	8	1	–	–	–	–	–	103	17.11
E. b. newmanii	–	–	1	5	26	167	348	412	261	216	102	27	2	1,567	20.21
Tennessee R.	–	–	–	2	8	81	158	166	43	8	1	–	–	467	19.38
Holston R.	–	–	–	–	1	19	41	50	10	1	–	–	–	122	19.43
Powell R.	–	–	–	1	1	5	7	11	3	–	–	–	–	28	19.25
Clinch R.	–	–	–	–	1	13	20	18	8	3	–	–	–	64	19.47
upper French Broad R.	–	–	–	–	3	12	9	4	–	–	–	–	–	28	18.50
Pigeon R., L. Pigeon R.	–	–	–	–	–	10	28	22	9	2	1	–	–	72	19.56
Little R.	–	–	–	–	1	6	19	15	2	–	–	–	–	43	19.26
lower Tennessee R.	–	–	–	1	1	16	34	46	10	2	–	–	–	110	19.46
Cumberland R.	–	–	–	–	–	2	11	39	72	110	51	14	2	301	21.65
S. Fork and upstream	–	–	–	–	–	2	8	21	22	24	7	–	–	84	20.94
downstream	–	–	–	–	–	–	3	18	50	86	44	14	2	217	21.92
St. Francis R.	–	–	–	–	–	5	25	28	10	4	1	–	–	73	19.81
Current-Black R.	–	–	–	1	3	24	42	48	13	3	1	–	–	135	19.40
upper White R.	–	–	–	–	–	1	3	12	35	48	27	11	–	137	21.83
L. Red R.	–	–	–	–	–	–	14	23	30	14	11	–	–	92	20.84
Arkansas R.	–	–	–	–	1	11	31	60	40	28	10	2	–	183	20.43
Ouachita R.	–	–	–	1	3	26	42	28	18	1	–	–	–	119	19.27
Saline R.	–	–	1	1	11	17	22	8	–	–	–	–	–	60	18.37
E. b. :newmanii × blennioides															
Green R.	–	–	–	23	51	61	28	4	1	–	–	–	–	168	17.65
E. b. blennioides	–	4	25	139	229	283	168	62	17	4	–	–	–	931	17.74
Ohio R.															
Salt R.-Harrod's Cr.	–	–	–	7	14	19	6	3	–	–	–	–	–	49	17.67
Kentucky R.	–	–	–	3	12	27	42	21	7	2	–	–	–	114	18.83
S. Fork–upstream	–	–	–	2	8	12	11	5	–	–	–	–	–	38	18.24
downstream	–	–	–	1	4	15	31	16	7	2	–	–	–	76	19.13
Whitewater R.-Miami R.	–	–	–	2	5	14	14	13	2	–	–	–	–	50	18.74
Licking R. (Ky.)	–	–	–	2	3	3	3	1	1	–	–	–	–	13	18.08
Scioto R.	–	–	1	17	32	32	10	4	2	–	–	–	–	98	17.54
Tygerts Cr. to Guyandot R.	–	–	–	8	9	6	3	–	–	–	–	–	–	26	17.15
Big Sandy R.	–	–	–	–	–	8	13	10	2	2	–	–	–	35	19.34
Kanawha R.	–	–	–	12	53	62	28	6	2	–	–	–	–	163	17.81
L. Kanawha, Big Wheeling Cr.	–	–	4	9	12	13	6	–	1	–	–	–	–	45	17.27
Muskingum R.	–	4	14	29	13	5	1	–	–	–	–	–	–	66	16.06
Monongahela R.	–	–	–	7	26	31	20	1	–	–	–	–	–	85	17.79
Allegheny R.	–	–	4	21	20	21	5	1	–	–	–	–	–	72	17.07
upper Genesee R.	–	–	1	16	16	12	7	1	–	–	–	–	–	53	17.21
Potomac R.	–	–	1	5	13	25	6	–	–	–	–	–	–	50	17.60
E. b. :newmanii × pholidotum															
Gasconade R.	–	–	–	3	12	19	16	3	–	–	–	–	–	53	18.08
E. b. pholidotum	7	157	248	338	102	26	4	–	–	–	–	–	–	882	15.53
Missouri race	–	4	34	122	77	25	4	–	–	–	–	–	–	266	16.36
Osage R.	–	4	23	75	23	5	–	–	–	–	–	–	–	130	16.02
Eastern Mo. group	–	–	11	47	54	20	4	–	–	–	–	–	–	136	16.70
Wabash-Gr. Lakes race	7	153	214	216	25	1	–	–	–	–	–	–	–	616	15.17

TABLE 4. LEAST CAUDAL PEDUNCLE SCALE COUNTS FOR MAJOR POPULATIONS OF *Etheostoma blennioides*.

Subspecies and River	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	N	x̄
E. b. gutselli	–	1	2	6	12	53	10	2	–	–	–	–	–	–	–	–	–	–	86	21.77
E. b. :gutselli × *newmanii*																				
Hiawassee R.	–	–	–	4	14	27	14	13	10	17	3	–	–	–	–	–	–	–	102	23.28
E. b. newmanii	–	–	–	–	8	34	57	111	270	430	304	150	131	90	20	11	–	1	1,617	26.43
Tennessee R.	–	–	–	–	1	–	6	16	80	185	112	37	23	6	1	–	–	–	467	26.32
Holston R.	–	–	–	–	–	–	–	5	30	56	20	10	1	–	–	–	–	–	122	26.02
Powell R.	–	–	–	–	–	–	1	1	1	8	7	5	4	–	–	–	–	–	27	26.85
Clinch R.	–	–	–	–	–	–	–	1	14	15	19	11	4	–	–	–	–	–	64	26.58
upper French Broad R.	–	–	–	–	–	–	2	4	6	10	6	–	–	–	–	–	–	–	28	25.50
Pigeon R., L. Pigeon R.	–	–	–	–	–	–	1	2	10	31	19	5	4	–	–	–	–	–	72	26.33
Little R.	–	–	–	–	–	–	–	1	7	15	18	1	1	–	–	–	–	–	43	26.33
lower Tennessee R.	–	–	–	–	1	–	2	2	12	52	24	6	8	2	1	–	–	–	110	26.42
Cumberland R.	–	–	–	–	–	–	–	1	6	30	32	58	69	76	19	11	–	1	303	28.71
S. Fork and upstream	–	–	–	–	–	–	–	1	6	25	18	16	11	7	–	–	–	–	84	27.23
downstream	–	–	–	–	–	–	–	–	–	5	14	42	58	69	19	11	–	1	219	29.27
St. Francis R.	–	–	–	–	–	2	1	4	25	27	11	1	2	–	–	–	–	–	73	25.66
Current-Black R.	–	–	–	–	1	1	8	16	52	42	17	1	–	–	–	–	–	–	138	25.29
upper White R.	–	–	–	–	–	–	2	5	7	25	47	30	26	7	–	–	–	–	149	27.28
L. Red R.	–	–	–	–	–	–	3	15	21	30	13	5	4	1	–	–	–	–	92	25.77
Arkansas R.	–	–	–	–	–	1	7	10	40	60	64	17	7	–	–	–	–	–	206	26.17
Ouachita R.	–	–	–	–	1	9	11	36	35	28	8	1	–	–	–	–	–	–	129	24.67
Saline R.	–	–	–	–	5	21	19	8	4	3	–	–	–	–	–	–	–	–	60	22.90
E. b. :newmanii × *blennioides*																				
Green R.	–	–	–	–	8	16	56	42	28	11	4	–	1	–	–	–	–	–	166	23.73
E. b. blennioides	–	–	2	15	65	198	270	231	122	55	9	3	–	–	–	–	–	–	970	23.32
Ohio R.																				
Salt R.-Harrod's Cr.	–	–	–	–	3	8	15	10	10	3	–	–	–	–	–	–	–	–	49	23.51
Kentucky R.	–	–	–	–	–	8	17	32	35	16	4	2	–	–	–	–	–	–	114	24.47
S. Fork—upstream	–	–	–	–	–	5	11	13	7	1	–	–	–	–	–	–	–	–	37	23.68
downstream	–	–	–	–	–	6	7	17	25	15	4	1	–	–	–	–	–	–	75	24.69
Whitewater R.-Miami R.	–	–	–	–	–	–	3	16	14	12	4	1	–	–	–	–	–	–	50	25.02
Licking R. (Ky.)	–	–	–	–	4	9	11	8	4	1	1	–	–	–	–	–	–	–	38	23.16
Scioto R.	–	–	–	–	9	24	21	29	7	8	–	–	–	–	–	–	–	–	98	23.26
Tygerts Cr. to Guyandot R.	–	–	–	–	–	13	8	5	–	–	–	–	–	–	–	–	–	–	26	22.69
Big Sandy R.	–	–	–	–	–	–	5	10	13	7	–	–	–	–	–	–	–	–	35	24.63
Kanawha R.	–	–	–	3	10	36	78	33	7	1	–	–	–	–	–	–	–	–	168	22.91
upper	–	–	–	3	8	30	50	22	5	–	–	–	–	–	–	–	–	–	118	22.81
lower	–	–	–	–	2	6	28	11	2	1	–	–	–	–	–	–	–	–	50	23.16
L. Kanawha, Big Wheeling Cr.	–	–	2	4	6	12	14	5	2	–	–	–	–	–	–	–	–	–	45	22.22
Muskingum R.	–	–	–	4	17	25	16	3	1	–	–	–	–	–	–	–	–	–	66	22.00
Monongahela R.	–	–	–	–	1	17	24	31	12	–	–	–	–	–	–	–	–	–	85	23.42
Allegheny R.	–	–	–	3	13	21	32	11	2	–	–	–	–	–	–	–	–	–	82	22.50
upper Genesee R.	–	–	–	1	1	12	14	13	8	3	–	–	–	–	–	–	–	–	52	23.40
Potomac R.	–	–	–	–	1	13	12	20	3	1	–	–	–	–	–	–	–	–	50	23.28
E. b. :newmanii × *pholidotum*																				
Gasconade R.	–	–	–	–	4	4	19	22	3	1	–	–	–	–	–	–	–	–	53	23.36
E. b. pholidotum	1	1	17	178	355	211	108	33	2	–	–	–	–	–	–	–	–	–	906	21.35
Missouri race	1	–	2	27	90	82	66	23	2	–	–	–	–	–	–	–	–	–	293	21.87
Osage R.	1	–	1	19	62	46	22	6	–	–	–	–	–	–	–	–	–	–	157	21.53
Eastern Mo. group	–	–	1	8	28	36	44	17	2	–	–	–	–	–	–	–	–	–	136	22.27
Wabash-Gr. Lakes race	–	1	15	151	265	129	42	10	–	–	–	–	–	–	–	–	–	–	613	21.10

river populations are assigned to the Arkansas race as distinct populations.

The Little Red River population differs considerably in meristic characters (other than scale counts) from populations of the upper White, Current-Black, St. Francis, and Cumberland rivers. It also differs in the shape of the head and snout, lacking the bulging cheeks, the long swollen snout, and flattened head; consequently it has a low occurrence of the long-rounded (1%) and overhung snout (30%). The Little Red River population, therefore, must be considered separate from the rest of the White River and St. Francis River populations. The similarity of the Little Red and Arkansas river forms has been noted above. Comparison of specimens from the Devil's Fork of the Little Red River and Cadron Creek (the most downstream tributary of the Arkansas River from which *E. b. newmanii* have been taken) shows similar head shape, body shape, and coloration. This similarity indicates a derivation of the Arkansas River population from the Little Red River population. The absence of *blennioides* from the lower Arkansas drainage may, therefore, be the result of the entry of the species through the headwaters of the Little Red River and a later movement upstream in the Arkansas River drainage. The Little Red River population must presently be recognized, therefore, as part of the Arkansas race, on the basis of similarities in head and body shape.

Dispersal.—*E. b. newmanii* and *E. b. gutselli* appear to be the most primitive forms of *E. blennioides,* based on the greater squamation and development of the lip tip in *b. newmanii,* and the presence of the frenum and prevomerine teeth in *b. gutselli,* and its apparent relict distribution.

The presence of *E. b. gutselli* in the Little Tennessee and Pigeon rivers and of the closely allied *E. swannanoa* in the upper Tennessee River, point to an origin of *E. blennioides* in the Tennessee River drainage. The peculiar distribution of *E. b. gutselli* (discussed in more detail in the section on that subspecies) indicates that in the past it may have been more widely distributed, possibly throughout the upper French Broad River System, and that *E. b. newmanii*—evolved in the lower areas of the Tennessee basin—invaded the highland area more recently. The Tennessee River *newmanii* have similar characteristics (Tables 2–9) and only small differences are apparent between such widely separated drainages as the Duck, Elk, Sequatchie, and Holston rivers. West of the Mississippi River, however, major differences exist among the populations in almost all the large rivers. Usually a greater amount of variation indicates a longer period of isolation and evolution. The flow of the Tennessee River, however, mostly through mountains or highlands probably presents much better conditions for movement of this darter; the character of the river leads to a lack of isolation of populations in major tributaries. The western populations, because of the sluggish current and silt characteristics of the lower segments of the St. Francis, White, Arkansas, and Ouachita rivers, have probably been isolated for a long time. The whole question of dispersal of *newmanii* is obscured by time and extensive geological changes.

For the reasons indicated, and because the presence of the distinct Tennessee and Cumberland races denotes a long period of isolation, it is likely that *E. b. newmanii* evolved east of the Mississippi River and subsequently moved westward during one or more migrations. The Mississippi River tributaries in Arkansas probably were populated before or early in the Pleistocene. Fenneman (1938:84–85, fig. 25) indicated that the Mississippi Embayment (the large trough between the bluffs along western Kentucky, Tennessee, and Mississippi on the east side, and southeastern Missouri, eastern Arkansas, and Louisiana on the west) is probably due to erosion more than subsidence. Just before the Pleistocene Epoch, the Mississippi River was probably on the same level as the adjacent uplands. Carving of this trough by the Mississippi, the old Tennessee, St. Francis, Black, White, Arkansas, and Ouachita rivers created such remnants as Crowley's Ridge—crescent-shaped and dissected by several channels (Fenneman, 1938: pl. 3, fig. 25)—extending from about Cape Girardeau, Missouri, to Helena, Arkansas. Fenneman (1938) and Marbut (1895) indicated that the Mississippi River flowed on the west side of Crowley's Ridge in the channel occupied by the present Black, White, and Cache rivers. The Ohio River flowed on the east side of the ridge in the present St. Francis channel, and the Tennessee River occupied the present channel of the Mississippi River. The Ohio also followed what is known as the Cache River sag across southern Illinois, 10–15 miles farther north than at present, and separated from the Cumberland as well as the Tennessee River, into which the Cumberland emptied. The three major rivers apparently joined in the region of Helena, Arkansas, at the foot of Crowley's Ridge. In high-water phases, the Mississippi River is believed to have cut several of the channels in the ridge and more than one may have existed at the same time, connecting with the Ohio. Other channels probably connected the Ohio and Tennessee. Fenneman (1938) further stated that it was probably in the late Pleistocene that the Mississippi River broke through into the Ohio basin in the channel at Thebes, Illinois, and probably not until the Mississippi agraded this part of the Ohio channel did the Ohio break through to the south to join the Tennessee River.

If the assumption of the origin of *blennioides* as somewhere in the eastern Appalachians is correct, it can be inferred that *E. b. newmanii* migrated down the Tennessee River, particularly since the river was apparently in a downcutting stage in the Pliocene and its lower course was undoubtedly much different from its present condition (velocity, depth, turbidity, *etc.*). *E. b. newmanii* may have entered the Cumberland River in the late Pliocene or early Pleistocene where it became isolated, and evolved into the Cumberland race. The Tennessee River race of *newmanii* may have moved farther downstream and entered the St. Francis, White, and Arkansas drainages (probably through the connecting channels of the Mississippi, Ohio, and Tennessee rivers) or perhaps only into the Arkansas and Little Red rivers, where the forms are closer to the Tennessee form in head shape and meristic characters. The Cumberland race of *newmanii* apparently moved downriver and populated the St. Francis, Current-Black, and upper White rivers.

Little doubt exists that either (or both) the St. Francis or Black River populations of *E. b. newmanii*, moved up the Mississippi River and populated the Meramec drainage and other streams in southeastern Missouri and gave rise to the Missouri population of *E. b. pholidotum.* The eastern Missouri population of *pholidotum* probably moved into the Ohio River after the Mississippi River broke through at Thebes, Illinois, and extended its range up the Ohio River and into the Wabash system before the Ohio broke through to the Tennessee River channel. The breakthrough at Thebes was placed by Fenneman (1938:89–90) as probably during the Illinoisan glacial period. This timing may explain why the Tennessee or Cumberland River forms are not in the Wabash River System. It does raise the question of why the northern subspecies (*pholidotum*) is not in some of the southern tributaries of the Ohio River, such as the Green River drainage (now apparently occupied by a population of *E. b.* :*newmanii* × *blennioides* intergrades which appear closer to *newmanii*). If the Ohio and Tennessee rivers were separate in southern Illinois until late Pleistocene, the Green River may have been (1) populated by headwater transfer of *E. b. newmanii* from the Cumberland, or (2) occupied by the Cumberland or Tennessee race of *newmanii*, which moved up the Ohio from the junction below Crowley's Ridge or other connecting channels in the late Pliocene or early Pleistocene. During such an early migration, *newmanii* may have also populated the Wabash, only to have been driven out by the later ice sheets. The Green River intergrade population probably resulted from a later downstream movement of *E. b. blennioides,* the Ohio River subspecies.

Etheostoma blennioides gutselli (Hildebrand)

Poecilichthys gutselli Hildebrand, 1932:78–80, pl. 3 (original description, Tuckasegee R., N. C.).

Etheostoma (*Etheostoma*) *gutselli.* Kuhne, 1939:93; Bailey and Gosline, 1955:16, 40 (vertebral counts); Eddy, 1957:219, fig. 527 (description and distribution, in part); Moore, 1957:186, 191 (description and distribution, in part); Lennon, 1962:6 (distribution, in part).

Etheostoma blennioides gutselli. Miller, 1965: 1234 (diss. abstr.).

Etheostoma (*Etheostoma*) *blennioides gutselli.* Collette and Knapp, 1967:63 (types).

Holotype.—Poecilichthys gutselli, USNM 92402; male, 70.3 mm; N. C., Swain Co., Tuckasegee R. at Ela; James S. Gutsell: 26 Aug. 1930. Counts for the holotype are: lateral-line scales 53; transverse scales 16; least caudal peduncle scales 22; D.XIII-14; P_1, 15-15; there is a distinct frenum, no lip tip, a large anterior naked area on the belly, nine lateral blotches, two prevomerine teeth, the cheeks are scaled but the opercles are naked.

Diagnosis.—E. b. gutselli differs from the other subspecies in usually lacking scales on the opercles, in having the premaxillary frenum typically well-developed, and in lacking the lip tip common to the other forms. This large-scaled form differs further from *E. b. newmanii* in having fewer dorsal spines,

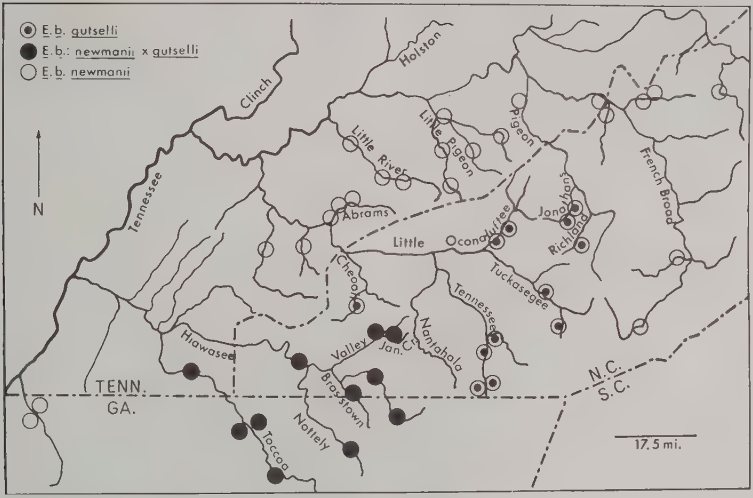

Fig. 4. Distribution of *Etheostoma blennioides gutselli, E. b. newmanii,* and *E. b.: newmanii × gutselli* in the Little Tennessee, Pigeon, and Hiawassee rivers. The distribution of *E. b. newmanii* in the French Broad, Little Pigeon, and Little rivers and Chicamauga Creek, Ga. is given to illustrate the limited distribution of *E. b. gutselli.* Each symbol indicates a collection area, but not all collections were plotted.

more dorsal rays (Table 1), and the anterior part of the belly scaleless in most specimens.

Distribution and relationships.—E. b. gutselli and *E. b. newmanii* occur allopatrically in the Little Tennessee and Pigeon rivers (Fig. 4). A detailed description of the topography of the Little Tennessee and Hiawassee River drainages can be found in Miller (1964). *E. b. newmanii* occupies the lower course of the Little Tennessee River (characterized by a relatively shallow gradient) and apparently never moved upstream any farther than Abrams Creek. The collections of *newmanii* from the lower Little Tennessee drainage (Abrams, Laurel, and Citico creeks) have typical *newmanii* characteristics (included in the lower Tennessee R. category in all tables). *E. b. gutselli* occupies the rest of the Little Tennessee System; specimens have been collected in tributaries of Cheoah River which joins the Little Tennessee only about 13 river-miles upstream from Abrams Creek. The allopatric distribution of these two forms apparently predates the construction of the huge TVA lakes on the Little Tennessee which today are effective barriers to either upstream or downstream migration of darters. Dr. Carl L. Hubbs made many collections in the Little Tennessee River System in the late 1930's and early 1940's, including several in Abrams Creek and the Cheoah and Oconaluftee rivers. Only *newmanii* was taken in Abrams Creek and only *gutselli* in the latter two areas. Lennon and Parker (1959:15) reported only *E. b. newmanii* from Abrams Creek in 1957 in an attempted reclamation of that stream for sport fishing. In 1962 and 1964, my attempts to collect *newmanii* were unsuccessful although many specimens of *Etheostoma rufilineatum* and *E. camurum* (Cope) were taken. It is possible that the 1957 "reclamation" wiped out the population of *newmanii.* If so, it represents another example of irreparable damage to a native fish fauna by the indiscriminate use of rotenone. The reclamation attempt proved futile because rough fish were reported in Chilhowee Lake (which receives Abrams Creek) in the fall of 1957, and 11 species besides rainbow trout (*Salmo gairdnerii* Richardson) were again present in Abrams Creek by September 1958. If *E. b. newmanii* was completely eliminated from Abrams Creek, the completion and flooding of Chilhowee Dam and Reservoir immediately after the reclamation attempt in 1957 blocked forever any potential upstream migration into Abrams Creek.

The Hiawassee River, the next major tributary of the Tennessee River from the east and downstream from the entrance of the Little Tennessee River, has much the same elevation, topography, and geologic history as the Little Tennessee System (Fig. 4). *E. blennioides* is represented in the Hiawassee drainage by a population that must be considered intergrades between *b. newmanii* and *b. gutselli.*

E. b. gutselli differs from *newmanii* most significantly in scale counts, opercle squamation, development of the frenum, and degree of belly squamation (Tables 1–4, 8). In his original description, Hildebrand (1932) gave the presence of prevomerine teeth ("teeth pointed, in bands on jaws, similar teeth on vomer") as one of the distinctive characters of *gutselli.* Examination of all known specimens, including the types, showed only a 47% occurrence of teeth on the prevomer and none on the palatines. The membrane covering the roof of the mouth had small villi-like projections to which Hildebrand may have referred. The differences in coloration and opercle squamation between *gutselli* and *newmanii* are probably great enough to warrant specific recognition of the former, were it not for *b. newmanii* × *b. gutselli* intergrades in the Hiawassee River.

On the basis of scale counts, dorsal spines and soft rays, lateral blotches, frenum, lip tip, and opercle scales, the Hiawassee population is intermediate between the two subspecies (Tables 1–4, 6, 8). The counts for left pectoral rays and degree of belly squamation differ from those of *newmanii* but resemble those of *gutselli* (Tables 7–8). Only in the occurrence of prevomerine teeth is the Hiawassee population (less than 10%) similar to *newmanii.* The color pattern of many specimens is darker and more irregular, like that of *gutselli,* but some specimens have the typical, well-defined lateral blotches on light background of *newmanii.* Generally the pattern is intermediate; blotching is more irregular on the dorsum than in *newmanii* and the average number of lateral blotches is higher; melanism is more pronounced but is usually not as heavy as in *gutselli.* The breeding color pattern of specimens taken in tributaries of the Toccoa River is similar to that of other subspecies except for greater melanism.

Lateral-line scale counts of specimens from the various tributaries of the Hiawassee River were plotted from upstream to downstream to test for clinal variation (summarized as upstream tributaries against the Toccoa River in Table 2). A decrease in number of lateral-line scales for the Toccoa River specimens may indicate isolation of this population from those in other Hiawassee River tributaries. Similar analysis of *b. gutselli* data showed no distinct clines or differences, which may reflect the nearly uniform high altitude of the portions of the Little Tennessee where *gutselli* is found.

Reconciliation of the distribution of *gutselli, newmanii,* and the Hiawassee River intergrades is a complex problem, complicated by the presence of populations of typical *gutselli* in Jonathan and Richland creeks of the Pigeon River drainage. Only four collections from these populations were available for study (UMMZ 131245, CU 42103, USNM 42430, CU 49738), but the characteristics of the 26 specimens were generally like those of *gutselli* from the Little Tennessee River. Color was in irregular blotches, the frenum was present, and the snout was longer than in *E. b. newmanii.* Four specimens were unique among *gutselli* in having complete belly squamation; two specimens had scales on the opercles, whereas only one other *gutselli* specimen (Tuckasegee River) had a scaly opercle.

Lateral-line scale counts of lower Hiawassee River [= Toccoa R.] specimens differ almost completely from those of *newmanii* taken in adjacent tributaries of the lower Tennessee River (Table 2), indicating little or no mixing of the two forms at present. The Hiawassee River population as a whole, however, shows considerable overlap of meristic data and color pattern with both *newmanii* and *gutselli.* To judge by present distribution, it appears that *gutselli* was in the Hiawassee River before *newmanii* and that the latter invaded that drainage, giving rise to the present intergrade population. If *gutselli* evolved in the Little Tennessee River System, it may have populated the Hiawassee River System through stream piracy. An area of possible stream piracy appears between the Valley River (Hiawassee drainage), and the Nantahala River (Little Tennessee drainage), near Topton, North Carolina.

Wright (1932:177) indicated that the dendritic pattern of some tributaries of the upper Valley River is irregular, but did not feel that stream flow had actually been reversed. An interpretation of the geomorphology of the Valley River–

Nantahala River region by Dr. R. D. Ross (pers. comm.), based on topographical maps, data presented by Keith (1907), and observations by Ross, indicates a strong probability that the present upper Valley River was once a large tributary of the Cheoah River when the upper Nantahala was the headwater of the Cheoah. The present course of the Nantahala most probably was brought about by a small pirate tributary of the Little Tennessee River that worked back through the soluble Murphy Marble in a northeast–southwest direction. This pirate stream —now the lower Nantahala River—finally broke through to the old headwaters of the Cheoah, and started that part of the river into a stage of fast downcutting. As downcutting progressed and created a northward-flowing river (the present lower Nantahala), it finally caused a major breakthrough by the present upper Nantahala (then upper Cheoah River) at the present 90° bend in the Nantahala—about 1.5 miles, southwest of Nantahala, North Carolina. Once this breakthrough was complete, the connection with the Cheoah River gradually dried up. Subsequently, the present lower Valley River worked back in a northeasterly direction until it captured the headwaters of present Nelson Creek (the old Valley Creek), leaving the latter as an unusually small, oddly located tributary of the Nantahala River. The area between the present headwaters of Valley River and Nelson Creek is flat and has the characteristics of a former piracy, such as water-rounded boulders.

The marked similarities between *gutselli* and the Hiawassee intergrades might be considered an adaptation to high altitude, were it not that specimens from the Hiawassee drainage that most closely resemble the *gutselli* type are not always from the highest altitudes. A comparison of the meristic data for *gutselli* and the Hiawassee River intergrades with those of *newmanii* generally shows a decrease rather than an increase in number of parts, except for more pectoral rays in the Hiawassee population. This trend is a reversal of the expected increase in number of parts of a structure because of altitude.

Another explanation of the origin of the intergrade population may be that *gutselli* was once more widespread than it is today, and that the present populations exist as relicts. This assumption means that the ancestral *blennioides* population split into two parts: the French Broad (including Little Tennessee, Pigeon, and Little Pigeon rivers) and Hiawassee drainage highland population that evolved into *gutselli*; and the more lowland Tennessee River population that evolved into *newmanii*. Subsequently, *newmanii* invaded the upstream (or highland) tributaries, giving rise to the allopatric distribution of the two subspecies in the Pigeon and Little Tennessee rivers (where it was able to outcompete the *gutselli* type in the lower parts of these rivers) and to the intergrade population in the Hiawassee River System.

Etheostoma blennioides blennioides Rafinesque

Etheostoma blennioides Rafinesque, 1819: 419 (original description, Ohio R.); Rafinesque, 1820a:169 (description); Rafinesque, 1820b:87 (description and distribution, in part); Kirtland, 1840:348 (misidentification-figured *Percina maculata*); Storer, 1848:103; Jordan, 1874:27 (misidentification, given under "blacksided darters" and from L. Mich.); Jordan, 1877a:17 (synonym of *Diplesium blennioides*); Jordan, 1890:142 (distribution); Woolman, 1892: 251, 259, 280, 284, 286 (distribution); International Commission of Zoological Nomenclature, 1910:25–27 (confirmed as type-species of genus); Jordan, 1916:25 (to replace *Diplesion* as generic name of *blennioides*); Jordan, 1917:86 (the type of *Etheostoma*); Fowler, 1919:70 (distribution, in part); Hankinson, 1923:33 (distribution); Jordan, Evermann, and Clark, 1930: 286 (synonymy and distribution, in part); Pratt, 1935:121–122 (description and distribution, in part); Schrenkeisen, 1938:223 (description, habits, distribution and synonymy, in part); Gerking, 1949:301, 304 (ecology); Eddy, 1957:209 (description and distribution, in part); Moore, 1957:186, 192 (description, diagnosis, and distribution, in part); Trautman, 1957:35–36 (synonymy, in part), 108 (in key to Ohio fishes), 550, 571–573 (diagnosis, distribution in Ohio, and habitat); Clay, 1962:134 (description and range).

Diplesium blennioides. Agassiz, 1848:362 (changed ending of genus from *-ion* to *-ium* as grammatically proper); Jordan and Copeland, 1876:133–136 (synonymy); Jordan, 1877a:15 (synonymy); Jordan, 1878a: 412, 439 (type-species of *Diplesium* and distribution, in part); Jordan, 1878b:222 (synonymy, description, and range, in part); Jordan, 1882:748 (synonymy), 751 (near Indianapolis, Ind.), 967 (synonymy, description, habitat, and habits); Boulenger, 1895:100 (synonymy, description, and range, in part).

Pileoma cymatogramma Abbott, 1860a:327 (original description, no locality given, holotype: ANSP 14009).

Percina cymatogramma. Abbott, 1860b:479 [*Percina* Haldeman (1842) senior synonym of *Pileoma* DeKay (1842)]; Fowler, 1907a: 522 (synonym of *Diplesion blennioides*).

Hyostoma blennioperca. Cope, 1869:215 (Kanawha R., Va., part of type-series = ANSP 14004, 14006–8, 14020–25); Vaillant, 1873:105 (Kanawha and Holston rivers); Fowler, 1907a:522 (largest specimen of *H. blennioperca* in type-series designated as the "type," Holston R., Va.).

Diplesion blennioides. Jordan, 1877b:10 (improper spelling, maintained modern usage = *Diplesium*), 22–24 (synonymy); Jordan and Gilbert, 1877:86 (synonymy, type of, = *Etheostoma blennioides*); Jordan, 1887: 866; Jordan and Evermann, 1896a:361 (synonymy and range, in part); Jordan and Evermann, 1896b:1052–1053, fig. 449 (description, color pattern, diagnosis, range, and synonymy); Fowler, 1907b:18 (Beaver R., Pa.); Fowler, 1907a:522 (synonymy, distribution, in part); Evermann, 1918:357 (synonymy, distribution in Ky. and Tenn.); Hankinson, 1927:484 (Allegheny R. tributaries, Allegheny State Park, N. Y.).

Etheostoma blennioides blennioides. Welter, 1938:68 (Licking R., Ky.); Raney, 1939: 276 (Western Pa.); Raney and Lachner, 1939:158 (species associate of *E. maculatum* in Shenango R., Pa.); Raney, 1941:12, 15 (compared with juvenile *E. kanawhae*); Gerking, 1945:13 (habitat), 96 (species associates and distribution, Ind.); Eddy and Surber, 1947:224–225 (description, distribution in northeast), Lachner *et al.*, 1950:93–111 (life history, Allegheny R. tributary, western Pa.); Bailey, 1951:189 (removed from Iowa faunal list); Ross, 1958:18 (comparison of distribution with *Campostoma anomalum pullum*); Ross, 1959:19, 26 (New-Kanawha R., Va.); Ross and Perkins, 1959:13–33 (distribution, New R., Va.); Trautman, 1961:88, 90, 92 population dynamics in central Ohio streams); Miller, 1965:1234 (diss. abstr.).

Types.—Call (1899:29) noted that Rafinesque did not preserve any type material. A photograph of a sketch of this species from Rafinesque's notebook (Collette and Knapp, 1967, fig. 1) shows a strong resemblance to specimens of the upper Ohio River form as here designated. Call (1899:31) further stated that Rafinesque made his "first really important collections at the Falls of the Ohio, a locality abounding in the smaller varieties, and remarkably rich in individuals of the genus *Etheostoma*." He pointed out that *Etheostoma flabellata* Rafinesque was described at this locality. Since *E. blennioides* was described in the same publication with *E. flabellata*, perhaps it was also first collected near the Falls. Counts from the sketch are as follows: D.XIII-13; A. II, 8; P_1 16; P_2 1–5; C. 20. Seven lateral blotches are visible, beginning at the posterior edge of the pectoral fin—two are under the first dorsal, three under the second dorsal, and two on the caudal peduncle. At least one and possibly two blotches should be hidden by the pectoral fin, indicating a count of eight or nine lateral blotches, common for this form. The blotches are the "ditto mark" type, more common for this form than for *E. b. pholidotum*.

Diagnosis.—*E. b. blennioides* differs from *E. b. gutselli* by having a scaly opercle and the lip tip separated from the snout by a deep groove. *E. b. blennioides* has more lateral-line scales ($\bar{x}$:65.42) than *E. b. pholidotum* ($\bar{x}$:59.56), and fewer than *E. b. newmanii* ($\bar{x}$:72.93). Transverse and least caudal peduncle scales differ from the other forms in the same way. *E. b. blennioides* also differs from *pholidotum* by having about a 60% occurrence of a naked area on the belly instead of 100% scaled as in *pholidotum*; it has fewer dorsal spines (mode: 13, $\bar{x}$:13.02) and soft rays (mode: 13, $\bar{x}$:12.89) than *newmanii* (mode: 13, $\bar{x}$:13.39 and mode: 13, $\bar{x}$:13.31 for dorsal spines and soft rays, respectively). It is distinct from *pholidotum* and *newmanii* in usually having a lip tip shorter than its width (S), more lateral blotches, and usually more dark-green lateral bands in breeding males (6–8, $\bar{x}$:7.68) than the other two forms (5–8, $\bar{x}$:7.45 for *pholidotum* and 7.29 for *newmanii*).

Distribution and relationships.—*E. b. blennioides* is restricted to the Ohio River and its north and south tributaries upstream from the confluence of the Green and Ohio rivers, the Potomac River, and the upper Genesee River (Fig. 3). In the Green River, which enters the Ohio from the south opposite Evansville, Indiana, *E. blennioides* occurs as intergrades (*newmanii* × *blennioides*). The Green River population resembles *newmanii* in number of anal rays,

Table 5. Anal Ray Counts for the Subspecies, Intergrades, and Certain Other Populations of *Etheostoma blennoides.*

Subspecies and River	6	7	8	9	10	N	x̄
E. b. gutselli	–	14	68	4	–	86	7.88
E. b. :gutselli× newmanii							
Hiawassee R.	–	9	63	16	–	88	8.08
E. b. newmanii	1	112	955	350	9	1,427	8.18
Tennessee R.	1	37	279	71	2	390	8.09
Holston R.	1	2	76	27	–	106	8.22
Clinch R.	–	3	22	20	–	45	8.38
upper French Broad R.	–	6	20	2	–	28	7.86
Pigeon R., L. Pigeon R.	–	10	50	11	1	72	8.04
Little R.	–	3	34	4	1	42	8.07
lower Tennessee R.	–	13	80	17	–	110	8.04
Cumberland R.	–	23	134	32	–	189	8.05
St. Francis R.	–	2	30	40	2	74	8.57
Current-Black R.	–	6	65	66	1	138	8.45
upper White R.	–	2	68	75	4	149	8.54
L. Red R.	–	7	75	10	–	92	8.03
Arkansas R.	–	16	158	32	–	206	8.08
Ouachita R.	–	15	98	16	–	129	8.01
Saline R.	–	4	48	8	–	60	8.07
E. b. :newmanii × blennioides							
Green R.	–	10	113	44	2	169	8.22
E. b. blennioides	1	140	683	148	–	972	8.01
Kanawha R.	–	30	117	21	–	168	7.95
upper	–	14	84	20	–	118	8.05
lower	–	16	33	1	–	50	7.70
Allegheny R.	–	16	58	8	–	82	7.90
upper Genesee R.	–	3	25	25	–	53	8.42
E. b. :newmanii × pholidotum							
Gasconade R.	–	5	36	12	–	53	8.13
E. b. pholidotum	1	63	520	299	7	890	8.28
Missouri race	1	52	199	40	–	292	7.95
Wabash-Gr. Lakes race	–	11	321	259	7	598	8.44
lower Genesee R.	–	1	31	16	–	48	8.31

dorsal spines, and soft rays, lateral blotches, and type of belly squamation (Tables 5–6, 8). It is closer to *blennioides* in counts of transverse and least caudal peduncle scales and in pectoral rays and lip tip (Tables 3–4, 8); it is intermediate in lateral-line scale counts and snout type (Tables 2, 9). The Green River flowed into the much smaller and shortened preglacial Ohio River that headed in southeastern Indiana or southwestern Ohio and flowed generally southwest to the Mississippi. Probably the Green River was populated by either the Tennessee or Cumberland race of *newmanii* originally, and has since been invaded by *blennioides* moving down the Ohio. *E. b. blennioides* also entered the Potomac River through stream piracy, and the upper Genesee River of New York and Pennsylvania by drainage modifications during glacial retreat.

All the populations in the Ohio River tributaries upstream from the mouth of Green River appear to belong to *E. b. blennioides,* although isolation and differentiation have apparently been effective for a considerable time (Tables 2–9). The data shows a general trend toward increasing lateral-line scale counts upstream and downstream from the Kanawha River, except the Big Sandy River population (Table 2). Transverse scale counts (Table 3) showed no clear trends, but counts of least caudal peduncle scales (Table 4) are like those of the lateral-line scales. I interpret this trend as an indication that the population in the Kanawha River (which exists as the remnant of the upper Teays River) probably gave rise to the upper Ohio River form of *E. b. blennioides,* by upriver and downriver dispersal. Inasmuch as *E. b. newmanii* could not have moved up the Ohio River until after at least the first glacial advance, and *E. b. blennioides* is present in the New-Kanawha River both above and below the Falls (at Kanawha Falls, W. Va.)—which were probably cut during the first major glacial recession—it is likely that the species gained access to the New River (old Teays River) by stream piracy with headwaters of the Tennessee River. Ross and Carico (1963:7–9) documented two cases of probable stream captures between the New and Holston (Tennessee River drainage) rivers. The specimens from below the Falls had slightly more lateral-line and least caudal peduncle scales, whereas the New River specimens (above the Falls) seem to have retained some characteristics of the Tennessee River form —more anal rays, dorsal spines and soft rays, fewer lateral blotches, and a higher proportion of type C [= completely scaled] belly squamation (Tables 2, 4–6, 8).

Thornbury (1958:399–400, fig. 16.9) described the preglacial drainage in the Ohio Valley. When the ice sheets moved southward over the Great Lakes region to the Ohio Valley, the preglacial Teays River was blocked and a new outlet was found by an overflowing of the old divides to the southwest (Thornbury, 1958:399), probably at the time of the first ice invasion (Tight, 1903:50). When the general present course of the Ohio had been established, the upper Ohio form, *E. b. blennioides,* moved downstream to populate river systems such as the Salt River and Harrod's Creek as well as to mix with the Green River population. It had maintained a glacial refugium in the southern tributaries of the Ohio.

Janssen (1952), who traced the history of the Teays River, indicated that it rose in the Appalachian Mountains near Blowing Rock (N. C.) and flowed generally northward. The upper part of the Teays followed the course of the present New River and most of the Kanawha River (the names change at Gauley Bridge, W. Va.) to near St. Albans, W. Va. (Tight, 1903:50), where it swung west to the Scioto Valley, flowed northward, and then swung westward across Indiana into Illinois. There the Teays followed the valley of the present Illinois and Mississippi rivers, and was joined by the Mississippi near Lincoln, Ill. (Janssen, 1952:74). While the Teays was in existence, the Monongahela River flowed approximately northward, through the reversed Beaver River (Tight, 1903:18) into a precursor of the St. Lawrence River (now the Lake Erie basin). The Allegheny River also flowed northeastward to this river. The lower Ohio River, small and separate from the Teays, flowed southwestward. During the first or subsequent glacial advances, the great ponding action caused the Allegheny and Monongahela to overflow to the southwest into the Teays River basin. The damming of the Teays, probably in one of the glacial advances, also caused it to overflow to the southwest, forming roughly the present course of the Ohio River. *E. b. blennioides* was then able to move from the Kanawha into the Monongahela and Allegheny systems and into downstream tributaries of the Ohio River.

The population in the Big Sandy River, originally a tributary of the Teays and presently an Ohio River tributary about 40 miles downstream from the Kanawha, shows major differences in all scale counts from other populations of *E. b. blennioides* (Tables 2–4). Because of the possibility of gene exchange through stream piracy, meristic data were compared for the Big Sandy population and *newmanii* from the Clinch and Powell rivers (Tennessee River drainage). Counts of lateral-line and transverse scales are similar in the three populations, but the Big Sandy population has fewer least caudal peduncle scales (Tables 2–4). Specimens from the Big Sandy River differ from both the Clinch and Powell samples in lip tip, belly squamation, dorsal spines and soft rays, pectoral rays, lateral blotches, and snout types; it appears that no gene exchange has ever occurred between these drainages (Tables 6–9). Woolman (1892:284) gave lateral-line counts for ten specimens from various tributaries of the Big Sandy (frequency of each count is in parentheses, if greater than one): 61, 64 (3), 65, 66, 68 (2), 69 (2). These counts are typical of the other populations of *E. b. blennioides,* and it is possible that the observed differences in the two collections I examined were due to environmental conditions.

The Kentucky River population also differs from other populations of *E. b. blennioides*; scale counts are higher (Tables 2–4), and the percentage of the long-rounded snout type is higher (Table 9). High scale counts may be indicative of the downstream increase for the Ohio tributaries, but the snout type indicates gene exchange with

TABLE 6. NUMBERS OF DORSAL SPINES AND SOFT RAYS FOR SUBSPECIES AND MAJOR POPULATIONS OF *Etheostoma blennioides.*

Subspecies and River	Dorsal Spines								Dorsal Soft Rays							
	11	12	13	14	15	16	N	x̄	11	12	13	14	15	16	N	x̄
E. b. gutselli	1	35	37	15	–	–	88	12.75	–	–	16	49	19	2	86	14.08
E. b. :gutselli × *newmanii*																
Hiawassee R.	–	25	64	14	–	–	103	12.89	–	4	35	58	6	–	103	13.64
E. b. newmanii	1	94	852	614	56	1	1,618	13.39	4	141	858	573	39	1	1,616	13.31
Tennessee R.	–	1	113	311	41	1	467	13.85	–	23	252	182	10	–	467	13.38
Holston R.	–	–	21	91	20	–	132	13.99	–	5	62	52	3	–	122	13.43
Powell R.	–	–	8	19	1	–	28	13.75	–	3	13	12	–	–	28	13.32
Clinch R.	–	–	20	35	9	–	64	13.83	–	3	34	27	–	–	64	13.38
upper French Broad R.	–	–	11	16	1	–	28	13.64	–	3	16	9	–	–	28	13.21
Pigeon R., L. Pigeon R.	–	–	18	51	3	–	72	13.79	–	5	41	25	1	–	72	13.31
Little R.	–	–	9	32	2	–	43	13.84	–	1	25	17	–	–	43	13.37
lower Tennessee R.	–	1	26	77	5	1	110	13.81	–	3	61	40	6	–	110	13.45
Cumberland R.	1	17	128	147	11	–	304	13.49	2	41	184	71	4	–	302	13.11
St. Francis R.	–	8	48	17	–	–	73	13.12	–	–	29	41	4	–	74	13.66
Current-Black R.	–	6	90	42	–	–	138	13.26	–	2	44	81	10	1	138	13.74
upper White R.	–	14	103	31	1	–	149	13.13	–	3	49	87	10	–	149	13.70
L. Red R.	–	8	69	15	–	–	92	13.08	–	5	45	40	1	–	91	13.41
Arkansas R.	–	23	158	23	2	–	206	13.02	1	31	129	45	–	–	206	13.06
Ouachita R.	–	13	95	20	1	–	129	13.07	1	21	88	19	–	–	129	12.97
Saline R.	–	4	48	8	–	–	60	13.07	–	15	38	7	–	–	60	12.87
E. b. :newmanii × *blennioides*																
Green R.	–	3	73	86	7	–	169	13.57	–	24	105	36	4	–	169	13.12
E. b. blennioides	4	143	640	163	2	–	952	13.02	18	218	568	143	2	–	949	12.89
Ohio R.																
Salt R.-Harrod's Cr.	–	10	32	7	–	–	49	12.94	–	7	30	12	–	–	49	13.10
Kentucky R.	1	16	77	20	–	–	114	13.02	1	19	82	13	–	–	115	12.93
Whitewater R.-Miami R.	–	8	20	21	1	–	50	13.30	3	15	24	8	–	–	50	12.74
Licking R. (Ky.)	–	8	27	3	–	–	38	12.87	–	4	29	5	–	–	38	13.03
Scioto R.	–	16	60	10	–	–	86	12.93	–	18	59	9	–	–	86	12.90
Tygerts Cr. to Guyandot R.	–	2	20	4	–	–	26	13.08	–	6	19	1	–	–	26	12.81
Big Sandy R.	1	7	19	8	–	–	35	12.97	–	11	22	2	–	–	35	12.74
Kanawha R.	2	20	126	20	–	–	168	12.98	–	38	98	32	–	–	168	12.96
upper	2	10	89	17	–	–	118	13.03	–	22	66	30	–	–	118	13.07
lower	–	10	37	3	–	–	50	12.86	–	16	32	2	–	–	50	12.72
L. Kanawha, Big Wheeling Cr.	–	8	30	7	–	–	45	12.98	4	11	27	3	–	–	45	12.74
Muskingum R.	–	10	42	14	–	–	66	13.06	1	35	34	6	–	–	66	12.68
Monongahela R.	–	11	59	15	–	–	85	13.05	1	22	52	11	–	–	86	12.85
Allegheny R.	–	11	55	16	–	–	82	13.06	4	26	37	10	–	–	77	12.69
upper Genesee R.	–	12	40	1	–	–	53	12.79	1	–	17	26	2	–	46	13.61
Potomac R.	–	2	35	13	–	–	50	13.22	2	14	32	2	–	–	50	12.68
E. b. :newmanii × *pholidotum*																
Gasconade R.	–	9	37	7	–	–	53	12.96	2	7	38	6	–	–	53	12.91
E. b. pholidotum	11	192	557	120	3	–	883	12.90	5	172	539	158	4	–	878	12.98
Missouri race	1	65	197	28	2	–	293	12.88	1	83	166	42	1	–	293	12.86
Osage R.	–	25	116	15	1	–	157	12.95	–	36	92	28	1	–	157	12.96
Eastern Mo. group	1	40	81	13	–	–	135	12.79	1	47	74	14	–	–	136	12.74
Wabash-Gr. Lakes race	10	127	360	92	1	–	590	12.91	4	89	373	116	3	–	585	13.04
lower Genesee R.	–	13	26	5	–	–	44	12.82	–	8	29	4	4	–	45	13.09

the Cumberland race of *newmanii* through stream capture. Kuehne and Bailey (1961) documented a major piracy of the upper part of the Collins Fork of the Kentucky River from its former connection with Little Richland Creek of the Cumberland drainage. This capture apparently involved a two-way transfer that allowed *newmanii* to enter the Kentucky River System and *blennioides* to enter the Cumberland River System (see also discussion of Cumberland River race of *E. b. newmanii*). Scale counts for the Kentucky River population, summarized for upstream and downstream samples, show a downstream increase for all three counts (Tables 2–4), opposite to the expected trend if Cumberland *newmanii* invaded the upper Kentucky to any great extent. But, two characteristics—counts of different lip tip sizes and numbers of lateral blotches for specimens found in the upper tributaries—are similar to those of *newmanii* (Table 8). The Kentucky River population, therefore, has been influenced by the Cumberland race, but apparently not to a great extent. The increased scale counts of downstream Kentucky River specimens indicate a possible invasion by the Green River form, but transverse and least caudal peduncle scale counts are higher than in the Green River population, and other counts show no strong similarities between the Green and Kentucky River populations. Because the Kentucky River also was originally a tributary of the Teays, it is likely that it was populated by *E. b. blennioides* sufficiently long ago to attribute the observed differences to isolation, subsequent evolution, and some gene exchange with the Cumberland River race of *E. b. newmanii.*

On the basis of all three scale counts, the Monongahela, Allegheny, upper Genesee, and Potomac river populations are similar (Tables 2–4). On dorsal fin-ray counts (Table 6), the Monongahela and Allegheny river populations are nearly identical; the situation was predictable from the postulated pattern of dispersal. Differences in lateral blotches and belly scales indicate a period of isolation of these two populations. Divergence of the Potomac River population from the Monongahela River population, indicates that the Potomac population has probably been isolated since it gained entry into the Potomac drainage through stream piracy with the Monongahela System. Ross (1952:85) documented a major capture between the Potomac and Youghiogheny rivers. The Savage River (Potomac River tributary) in Garrett County, Md., was described as having cut back between Backbone and Big Savage mountains (at approximately 1400 ft elev.) and diverted about 80 square miles of the Youghiogheny drainage into the Potomac drainage. Ross indicated that the Potomac River race of *Campostoma anomalum* gained entry by this route. According to Schwartz (1965), *E. b. blennioides* is present in the Monocacy and Conococheague rivers (centrally located among northern tributaries of the Potomac River), but it has not been found farther west in any northern tributaries. The subspecies has been taken in most southern tributaries of the Potomac River that lie to the west of the Shenandoah River, but apparently is not present in any southern tributaries east of and including the Shenandoah River System. Schwartz (1965) indicated a possible stream piracy between the North Fork of the South Branch of the Potomac River (where *blennioides* is abundant) and a tributary of Shavers Fork of the Cheat River (Monongahela System) near Harmon, W. Va. He maintained that *blennioides* gained access to the Potomac River System in this area. The lack of records of *blennioides* from the Youghiogheny River System supports his view, but mine pollution or other factors may have eliminated it from the Youghiogheny River in recent times and *blennioides* may have entered the Potomac System from that river.

The population in the upper Genesee River differs from the Allegheny River population in anal rays ($\bar{x}$ 8.42 and 7.90), a result of the complete separation of these two populations since the closing of the Cuba post-glacial outlet in southwestern New York (the apparent route of entry into the upper Genesee River by *E. b. blennioides*). This point is discussed further under distribution of *E. b. pholidotum*, which occupies the lower Genesee River and its tributaries.

Etheostoma blennioides ***pholidotum***
new subspecies
Fig. 5

Etheostoma blennioides. Nelson, 1876:35 (misidentification, = *E. blennioides* of Kirtland = *Percina maculata*): Jordan,

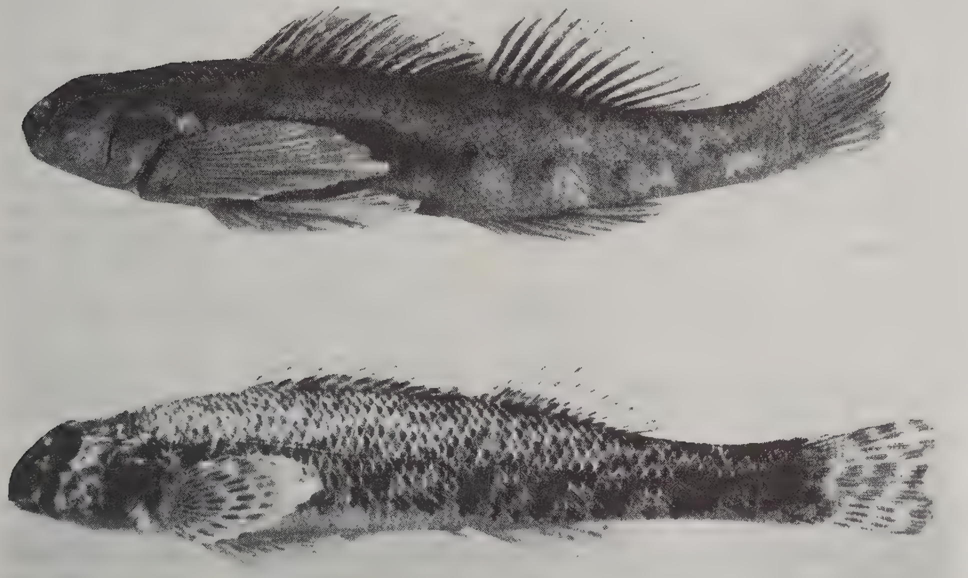

Fig. 5. *Etheostoma blennioides pholidotum.* Upper, male, CU 42251; Vermilion Co., Bean Cr., tributary to Middle Fork R., Wabash dr.; 30 April 1962. Lower, female, CU 8948; 52.0 mm; N. Y., Monroe Co., Sandy Cr. at first bridge above mouth, L. Ontario dr.; 10 June 1940.

1878c:51 (of Kirtland and of Agassiz and later writers as synonym of *Alvordius aspro* = *Percina maculata*); Evermann and Jenkins, 1888:50, 54 (several tributaries of Wabash R.); Jordan, 1890:159, 167 (Tippecanoe and White rivers of Wabash drainage); Meek, 1891:119, 123, 125 (Meramec, Big and Little Dry Fork rivers; Lock Fork, Osage Fork, and Little Piney rivers of the Osage drainage); McCormick, 1892: 29 (Vermilion R. and Sandusky Bay); Eigenmann, 1894:102 (distribution, Ind.); Kirsch, 1894:39 (Eel R., Wabash drainage); Kirsch, 1895:331, 336–337 (Maumee R. drainage); Hankinson, 1923:33 (Lake Erie tributaries of western N. Y.); Hankinson, 1924:58, 62, 63, 66, 78 (Cazenovia and Tonawanda creeks, Niagara R. drainage); Hubbs, 1926:68–69; Greeley, 1927: 65 (Genesee R.); Hubbs and Greene, 1928: 385, 391 (*Hyostoma newmanii* as synonym of, and present in Great Lakes); Hubbs and Brown, 1929:2 (mode of distribution, in southern tributaries of Lake Ontario), 51 (distribution in Ontario); Greene, 1935: 190 (range in part, visual records in Wis.—"presence in Wisconsin to be expected"); Goodnight and Wright, 1940:176 (species associate of *E. camurum* in Salt Fork of Wabash R.); Carlander, 1941:44 (synonymy, in part, Minn. record doubtful); Radforth, 1944:51 (range, habitat, Ontario distribution and mode of entry); Dymond, 1947:26; Larimore *et al.*, 1952:8, 12, 15, 16, 23 (habitat and ecology, species associates, distribution); Scott, 1954:93 (description, distribution, habits, and food); Bailey and Gosline, 1955:16, 21 (vertebral counts); Trautman, 1957:571–573 (diagnosis, distribution in Ohio); Underhill, 1957:23 (reviewed Minn. reports, suggested removal from Minn. faunal list); Winn, 1957:25 (reproductive behavior); Winn, 1958b:199–200 (reproductive behavior); Winn, 1958a:156–163 (reproductive behavior and ecology); Eddy and Underhill, 1959:343 (removed from Minn. faunal list); Larimore *et al.*, 1959:266, 271–273 (ecology, Ill. streams); Larimore and Smith, 1963:326–359, fig. 62 (ecology in Embarrass and Vermilion rivers, Ill.); Miller, 1965:1234 (diss. abstr.).

TABLE 7. NUMBER OF LEFT PECTORAL FIN RAYS FOR CERTAIN GROUPS OF *Etheostoma blennioides*.

Subspecies and River	13	14	15	16	17	N	$\bar{x}$
E. b. gutselli	–	8	66	11	–	85	15.04
E. b. gutselli × *newmanii*							
Hiawassee R.	–	3	32	62	4	101	15.66
E. b. newmanii	2	103	313	25	–	443	14.81
Powell R.	–	10	18	–	–	28	14.64
Clinch R.	–	24	39	–	–	63	14.62
E. b. blennioides							
Big Sandy R.	–	18	16	1	–	35	14.51

Diplesium blennioides. Jordan, 1877c:377 (White R., Ind.); Jordan, 1878c:43 (White R., Ind., and lower Wabash R.); Jordan 1878d:40 (Wabash Valley).

Diplesion blennioides. Cragin, 1885:105 (Wildcat Cr., Osage R. drainage); Graham 1885:76 (Wildcat Cr., synonymy, in part); Evermann, 1902:96 (Great Lakes); Evermann and Kendall, 1902:215 (Sandy Cr. at N. Hamlin, N. Y.); Bean, 1903:512–513 (misidentification—described *E. b. newmanii,* color pattern); Forbes, 1907:280–303 (habitat, ecology, species associates); Forbes, 1909:389, 400, 414, 421, 431 (range, distribution, ecology, Ill.); Hankinson, 1910:4 (Kickapoo Cr., Wabash drainage); Meek and Hildebrand, 1910:323 (description, range); Hankinson, 1913:111 (abundance, Embarrass R., Wabash drainage, ecology); Forbes, 1914:17 (ecology); Forbes and Richardson, 1920:292–293 (synonymy, in part, description, color pattern, distribution, habits, Ill.); Evermann and Clark, 1920:440–441 (description, color pattern, and habits); Cahn, 1927:53 (occurrence in Wisc., description of habits and identification from visual observation [probably a misidentification]); Thompson and Hunt, 1930:32, 37, 45, 64–65, 94 (distribution, habitat, ecology, Champaign Co., Ill.).

Etheostoma blennioides blennioides. Hubbs and Lagler, 1939:31 (key to Great Lakes fishes); Hubbs and Lagler, 1941:71, 76 (in key, range in Great Lakes drainage); Gerking, 1945:96 (distribution, Ind.); Eddy and Surber, 1947:224–225 (description, distribution, northeast); Scott, 1949:178 (species associates in Tippecanoe R.); Schockley, 1949:255, 269 (ecology, Sugar Cr., Wabash drainage); Fahy, 1954:139–205 (life history); Hubbs and Lagler, 1958:104, 109 (in key, northern distrib., S. E. Wis., Chicago, Iowa records regarded as incorrect; habitat).

Types.—Holotype CU 45466; 53.0 mm male; Illinois, Vermilion County, Bean Creek, tributary of Middle Fork River, 1.0 mile E of Potomac; 30 April 1962; Philip W. Smith, R. V. Miller, L. W. Knapp; RVM 198. Paratypes, 20 small to large adults from 39.5 to 75.0 mm SL, taken with the holotype and catalogued as CU 42251 (14) and USNM 197701 (6).

Counts for the holotype are as follows: dorsal fin rays XIV-14; anal rays II, 8; pectoral rays 15-15; lateral-line scales 60; transverse scales 15; least caudal peduncle scales 20; lateral blotches 7; lip tip length shorter than width (S); belly completely scaled (type C); snout type rounded but somewhat blunt and not overhung. The nape, opercles, and cheek are fully scaled, the breast is naked. The holotype is a young breeding male with very slight tubercle development on the posterior part of the belly.

Diagnosis.—Differs from *E. b. gutselli* by having a scaly opercle and completely scaled belly; from *E. b. blennioides* in having the belly fully scaled and in having lower lateral-line scale counts; and from *E. b. newmanii* by having lower scale counts, fewer dorsal spines, and predominantly no lip tip (A) or lip tip length shorter than width (S). Observations of highly colored males from throughout the range of the species indicate fewer dark-green lateral bands than for *E. b. blennioides.*

Etymology.—The name *pholidotum* is derived from the Greek *pholidotos* (scaled) and refer to the fully scaled belly.

Distribution and Relationships.—*E. b. pholidotum* occurs in the Osage River drainage in western Missouri (tributary to the Missouri River from the southwest), the Meramec drainage, Saline Creek, and possibly other small streams that enter the Mississippi River in east-central Missouri. Intergrades of *pholidotum* × *newmanii* are present in the Gasconade River System of south-central Missouri. *E. b. pholidotum* is absent from southern Illinois, but present in the Wabash drainage, the Maumee River, the Detroit and Cass river drainages of Michigan, the Thames River System of southwestern Ontario, the southern tributaries of Lakes Erie and Ontario, the lower Genesee River in western New York, and the Seneca and Mohawk rivers in central New York (Fig. 3).

Two races are recognized within this subspecies: the Missouri race, including the populations in Missouri except the Gasconade River population, and the Wabash–Great Lakes race, including the populations in the Wabash River and the Great Lakes drainage listed above.

All three scale counts for the Gasconade River population are higher than those of either the Osage population or the Meramec-Saline (eastern Missouri) group, but lower than those of the Current-Black River population which has the lowest counts of the Black-upper White-St. Francis populations of *E. b. newmanii* (Tables 2–4). The Gasconade River population is intermediate, on the basis of anal rays, lip tip, and snout type, between the Current-Black *newmanii* population and the Missouri race of *E. b. pholidotum* (Tables 5, 8–9). On number of dorsal spines and soft rays, and lateral blotches, the Gasconade River form closely resembles the Missouri *pholidotum* (Tables 6, 8). The shape of the head and snout in most Gasconade specimens is similar to the Cumberland race of *newmanii*—the head appears somewhat flattened and the cheeks bulge; the face just above the upper lip bulges as though swollen, and frequently the snout is overhanging (Fig. 1f). The long-rounded snout type is also associated with this head shape (discussed under *E. b. newmanii*). The Osage and eastern Missouri populations lack the bulbous snout and have less flaring cheeks. Some specimens from the Osage drainage tend to have a somewhat swollen snout and the occurrence of the overhung condition is slightly higher in this population than in the Meramec River—some mixing of the Gasconade type in the Osage River is suggested. Evidently the Gasconade population is an intergrade between the Cumberland race of *newmanii* and the Meramec River population of *pholidotum*. No evidence was found for headwater crossover between the Current and the Gasconade rivers but both have their headwaters on the Ozark Plateau of south-central Missouri. On the basis of the completely scaled belly and the three scale counts—intermediate between the Meramec and Current-Black River counts—it appears that either the St. Francis or Current-Black population gave rise to the Gasconade population, which in turn has since been invaded by the Meramec population. On the basis of the completely scaled belly and because the St. Francis River is geographically closest to the Meramec River, the Meramec River population appears to have originally derived from the St. Francis form. Possibly the St. Francis River population of the Cumberland race of *E. b. newmanii* moved up the Mississippi and Missouri rivers populating the southern tributaries of the Missouri and, while the Gasconade population retained its *newmanii* characteristics, the Meramec population differentiated. Later the Meramec population may have moved farther up the Missouri, mixed with the Gasconade population, and invaded the Osage drainage. The Osage River population definitely seems to have derived from the Meramec form that moved up the Missouri River.

The Missouri race has higher scale counts, more pectoral rays, and a greater occurrence of breast scales (39%) than the Wabash–Great Lakes race (less than 5%), but the latter averages more anal rays and lateral blotches (Tables 2–5, 7–8). On the basis of belly squamation, generally low scale counts, and similarity of body and head shape, these two races are included under *pholidotum*.

The differences between the two races of *pholidotum* indicate a considerable period of separation. The Wabash–Great Lakes race apparently is derived from the Missouri race because lateral-line scale counts for the Wabash River population are the highest for that race and close to those of the eastern Missouri population or the whole Missouri race. The degree of difference is only slightly greater than that between some of the different populations of the Wabash–Great Lakes race from drainage to drainage in a northeasterly cline (Table 2). The observed cline, however, is not environmentally induced. Such a cline usually shows an increase of scales or other structural parts that coincides with a decrease in temperature because of latitude or altitude (Bailey and Gosline, 1955, and others). In the Wabash–Great Lakes race, populations north and east of Michigan would be subjected to colder temperatures than the Wabash and Maumee populations (this difference would be compensated by a slightly later spawning time of the more northerly populations). Yet the "prairie type" streams of Indiana and Illinois usually warm faster, leading to more

TABLE 8. LIP TIP SIZE, DEGREE OF BELLY SQUAMATION, AND NUMBERS OF LATERAL BLOTCHES FOR THE SUBSPECIES AND MAJOR POPULATIONS OF *Etheostoma blennioides*. (Mode in boldface.)

Subspecies and River	Lip Tip*				Belly Squamation**					Lateral Blotches						
	A	S	L	N	LNA	SNA	C	I	N	6	7	8	9	10	N	x̄
E. b. gutselli	Frenum			78	**60**	22	4	–	86	1	3	23	26	1	54	8.43
E. b. :gutselli × newmanii																
Hiawassee R.	**78†**	25	–	103	**63**	20	5	2	90	3	68	29	3	–	103	7.31
E. b. newmanii	72	380	**1,089**	1,541	161	285	**1,114**	26	1,586	21	942	423	65	5	1,456	7.38
Tennessee R.	8	54	**350**	412	20	48	**369**	11	448	7	314	84	13	1	419	7.25
Holston R.	–	4	80	84	4	17	81	1	103	–	72	18	2	–	92	7.24
Powell R.	–	1	26	27	2	9	17	–	28	–	25	2	1	–	28	7.14
Clinch R.	1	6	54	61	4	8	47	5	64	3	52	9	–	–	64	7.09
upper French Broad R.	–	7	13	20	6	2	20	–	28	–	22	5	–	–	27	7.25
Pigeon R., L. Pigeon R.	4	19	49	72	3	8	57	4	72	2	47	20	3	–	72	7.33
Little R.	–	4	39	43	1	1	40	1	43	–	29	10	4	–	43	7.42
lower Tennessee R.	3	14	89	106	–	3	107	–	110	2	67	20	2	1	92	7.27
Cumberland R.	20	23	**259**	302	34	40	**224**	4	302	8	186	51	15	1	261	7.29
S. Fork and upstream	16	19	48	83	25	19	36	3	83	1	22	23	9	1	56	7.77
downstream	4	3	210	217	9	21	188	1	219	7	164	28	6	–	205	7.16
St. Francis R.	1	3	70	74	–	–	74	–	74	1	39	30	3	1	74	7.51
Current-Black R.	–	3	132	135	–	–	138	–	138	–	76	45	1	–	122	7.39
upper White R.	1	5	128	134	–	12	128	–	140	–	30	86	16	2	134	7.93
L. Red R.	12	72	8	92	26	56	10	–	92	2	51	26	4	–	83	7.39
Arkansas R.	8	109	87	204	7	46	141	6	200	2	157	31	6	–	196	7.21
Ouachita R.	22	96	10	128	65	51	12	4	132	1	56	44	6	–	107	7.51
Saline R.	–	15	45	60	9	32	18	1	60	–	33	26	1	–	60	7.47
E. b. :newmanii × blennioides																
Green R.	23	**102**	32	157	2	1	**164**	2	169	–	137	25	1	–	163	7.17
E. b. blennioides	297	**509**	97	903	168	330	**381**	93	972	4	471	322	144	16	957	7.68
Ohio R.																
Salt R.-Harrod's Cr.	10	34	5	49	1	9	28	11	49	2	40	7	–	–	49	7.10
Kentucky R.	26	66	23	115	65	32	5	13	115	2	92	20	1	–	114	7.16
S. Fork—upstream	–	23	15	38						1	35	3	–	–	39	7.05
downstream	26	43	8	77						1	57	18	1	–	77	7.25
Whitewater R.-Miami R.	8	39	3	50	14	31	3	2	50	–	28	21	1	–	50	7.46
Licking R. (Ky.)	12	18	8	38	11	9	17	1	38	–	37	1	–	–	38	7.03
Scioto R.	18	52	28	98	–	24	65	9	98	–	46	31	9	–	86	7.57
Tygerts Cr. to Guyandot R.	5	19	2	26	16	9	98	–	26	–	18	8	–	–	26	7.31
Big Sandy R.	31	4	–	35	2	24	9	–	35	–	8	15	9	3	35	8.20
Kanawha R.	95	42	5	142	24	37	75	32	168	–	63	74	27	4	168	7.83
upper					16	12	67	23	118	–	55	51	12	–	118	7.64
lower (1 spec. with 11 lat. blotches)					8	25	8	9	50	–	8	23	15	3	50	8.32
L. Kanawha, Big Wheeling Cr.	20	17	2	39	5	20	17	3	45	–	30	12	3	–	45	7.40
Muskingum R.	17	49	–	66	1	20	40	5	66	–	40	19	7	–	66	7.50

* A = tip absent.
S = tip length shorter than width.
L = tip length longer than width.
** LNA = large naked area, 30–50%.
SNA = small naked area, 15–30%.
C = completely scaled.
I = completely scaled but anterior scales imbedd.d.
† = predominantly a full frenum as in *gutselli*.

TABLE 8. *Continued.*

Subspecies and River	Lip Tip*				Belly Squamation**					Lateral Blotches						
	A	S	L	N	LNA	SNA	C	I	N	6	7	8	9	10	N	x̄
E. b. blennioides (continued)																
Ohio R. (continued)																
Monongahela R.	15	63	5	83	21	51	13	–	85	–	25	39	19	2	85	7.98
Allegheny R.	28	22	9	59	1	15	53	13	82	–	10	26	40	3	80	8.49
upper Genesee R.	8	29	6	43	–	28	25	–	53	–	5	20	24	4	53	8.51
Potomac R.	1	37	–	38	–	19	29	2	50	–	21	25	4	–	50	7.66
E. b. newmanii × pholidotum																
Gasconade R.	1	6	45	52	–	–	53	–		1	35	7	–	1	44	7.20
E. b. pholidotum	386	350	131	867	–	–	893	–		9	556	256	17	1	839	7.34
Missouri race	39	153	91	283	–	–	293	–		5	214	30	–	1	250	7.11
Osage R.	13	81	53	147	–	–	157	–		2	123	21	–	–	146	7.13
Eastern Mo. group	26	72	38	136	–	–	136	–		3	91	9	–	–	103	7.06
Wabash-Gr. Lakes race	347	197	40	584	–	–	600	–		4	342	226	17	1	590	7.44
lower Genesee R.					–	–	48	–		–	17	30	1	–	48	7.67

rapid development of fish eggs; these populations would be expected to have the lower scale counts. The fact that the cline decreases with more northerly latitude eliminates temperature as the cause of the northeasterly decrease in scale counts.

The present Meramec River population in southeastern Missouri at one time may have been part of an east-central Missouri population along with stocks in Saline Creek and other short streams tributary to the Mississippi River. After one of the three glacial periods "preceding" the Wisconsin, probably part of the east-central Missouri population moved across and, at the same time, up the Mississippi basin to populate the Wabash River and the upper Mississippi River area. During the Wisconsin glaciation, the Mississippi River population would have been driven back southward and the Wabash population, which would have been driven considerably downstream, could have found refuge in the lower reaches of the river—the Wisconsin ice sheet apparently did not advance farther south than about half the length of Illinois and Indiana in the Wabash basin (Forbes and Richardson, 1920:map 3; Gerking, 1945:map 1). Glacial meltwater conditions throughout southern Illinois probably made that area habitable for this darter then, but it apparently is not now.

Gerking (1945:map 96) and Forbes and Richardson (1920:map 89) showed that *blennioides* was absent from the unglaciated lower Wabash River, southern Illinois, and southwestern Indiana. Jordan (1890:160) pointed out that the lower Wabash tributaries "are mostly sluggish and yellow with clay and mud." Gerking indicated similar observations and associated the lower Wabash–Ohio River floodplain area with the Mississippi valley lowlands. Lowland, turbid conditions provide very poor habitat for the greenside darter (Trautman, 1957:572–573), thus the absence of the species from southern Illinois and tributaries of the lower Wabash is not surprising. These conditions do not rule out a derivation of the Wabash–Great Lakes race from the Missouri race. Jordan (1890) cited the occurrence and abundance of several species in the lower Wabash (among them *Percina uranidea* (Jordan and Gilbert) and *Etheostoma histrio* Jordan and Gilbert, that are more widely distributed west of the Mississippi River in Missouri and Arkansas. The presence of *E. b. pholidotum* in only the Wabash drainage in Illinois and no farther north than the Missouri River in tributaries of the Mississippi River, indicates that this form was already established in the Wabash drainage and did not move when the Mississippi River and Chicago routes were open during Wisconsin deglaciation.

Alternatively, this population may have moved through the ponded waters across the front of the Wisconsin ice sheet while the ice sheet was at, or near, its southern limit, or the migrating population may have used the Chicago outlet into the Great Lakes, but both of these possibilities appear remote. Flint (1947:254) placed the Lake Chicago stage (and its outlet through the present Illinois River valley) a little later than the Lake Maumee stage, but Hough (1963:90) indicated that the outlet of early Lake Chicago and the highest Lake Maumee stage

TABLE 9. SNOUT TYPE AND FREQUENCY OF OVERHUNG SNOUT FOR THE SUBSPECIES AND MAJOR POPULATIONS OF *Etheostoma blennioides.* Boldface = mode; LR = long rounded snout, BR = bluntly rounded snout, R = rounded snout, O = overhung, NO = not overhung.

Subspecies and River	Snout Type				Overhung		
	LR	BR	R	N	O	NO	N
E. b. gutselli	**22**	8	8	38	–	86	86
E. b. :gutselli × newmanii							
Hiawassee R.	**50**	32	8	90	2	**50**	52
E. b. newmanii	329	366	**619**	1,314	**762**	650	1,412
Tennessee R.	86	44	**207**		61	**277**	
Holston R.	22	6	43		14	57	
Powell R.	7	–	21		9	18	
Clinch R.	2	8	33		4	39	
upper French Broad R.	–	1	19		–	20	
Pigeon R., L. Pigeon R.	16	8	30		11	45	
Little R.	17	3	23		10	33	
lower Tennessee R.	22	18	39		13	66	
Cumberland R.	**74**	43	56		**254**	28	
St. Francis R.	20	10	40		56	13	
Current-Black R.	60	49	22		124	10	
upper White R.	56	55	12		109	22	
L. Red R.	1	23	68		28	64	
Arkansas R.	18	82	105		63	140	
Ouachita R.	14	58	51		30	73	
Saline R.	1	1	58		37	23	
E. b. :newmanii × blennioides							
Green R.	22	65	**70**		43	**114**	
E. b. blennioides	52	**436**	384	872	85	**530**	615
Ohio R.							
Salt R.-Harrod's Cr.	5	20	24		21	28	
Kentucky R.	25	6	34		37	78	
S. Fork—upstream	13	2	23		24	14	
downstream	12	4	61		13	64	
Whitewater R.-Miami R.	–	18	32		3	47	
Licking R. (Ky.)	–	1	37		2	36	
Scioto R.	9	74	3		10	30	
Tygerts Cr. to Guyandot R.	3	5	18		1	25	
Big Sandy R.	–	35	–		–	–	
Kanawha R.	–	130	12		2	63	
L. Kanawha, Big Wheeling Cr.	–	19	17		2	18	
Muskingum R.	–	40	26		–	42	
Monongahela R.	2	14	69		3	82	
Allegheny R.	–	45	3		–	–	
upper Genesee R.	3	16	27		1	34	
Potomac R.	5	1	32		2	36	
E. b. :newmanii × pholidotum							
Gasconade R.	15	10	**27**		**37**	15	
E. b. pholidotum	12	**617**	208	837	86	**481**	567
Missouri race	4	**139**	135		28	**217**	
Osage R.	1	75	68		32	124	
Eastern Mo. group	3	64	67		5	93	
Wabash-Gr. Lakes race	8	**478**	73		58	**264**	

(with its outlet down the Wabash River) were contemporaneous. If Flint's estimate of the timing is followed, it would indicate that *pholidotum* must have moved out of the established areas in eastern Missouri and used the Wabash outlet exclusively *before* the Chicago outlet existed. This is contradicted, however, by Hough's estimate of the timing of the two outlets as being contemporaneous. Following Hough's estimate, if *pholidotum* moved at the start of the recession of the Wisconsin, it is unlikely that it would have failed to migrate up the Mississippi River to the present Illinois confluence (a relatively short distance).

The similarity of characteristics and the northeastward decrease in number of lateral-line scales clearly indicate that the Wabash River population used the Maumee outlet during one substage or more of the Lake Maumee stage of Wisconsin deglaciation. The Wabash River population spread along the southern Lake Erie basin and into southeastern Michigan and southwestern Ontario. Hough (1963:91) indicated that following the highest Lake Maumee stage, at least two glacial readvances and recessions opened a channel across the Michigan peninsula through the Grand River channel into Lake Chicago (now Lake Michigan). It is not clear why—if *pholidotum* was present in Lake Maumee at the first substage—it did not reach Lake Michigan via the Grand River channel. One reason might be that the edge of the ice sheet was too close to this channel (Hough, 1963:figs. 3a–3d), and extremely cold temperatures may have kept *pholidotum* from moving far enough up Lake Maumee to enter the Grand River; alternatively, although present in the Wabash River before the first (or highest) Lake Maumee stage, the subspecies might not have entered that lake until the last readvance and opening of the Maumee outlet, shortly after which the Grand River channel was closed. During the next stages in glacial recession (Lakes Whittlesey and highest to lowest Warren) *pholidotum* probably moved across the present Lake Erie basin into northeastern Ohio. Flint (1947:255–259) and Hough (1963:93–95) indicated that these lakes covered the Huron–Erie basin east to western New York.

Hough (1963:93–97, figs. 4d–f, 5a–b) showed that during the lowest Lake Warren–Lakes Grasmere through Algonquin stages, the pro-glacial lake had a connection with an eastward drainage across central New York. That outlet ran through the present Mohawk–Hudson River System. It must have been at that time that *pholidotum* moved across the Niagara front and into central New York, finding its way into the lower Genesee, Seneca, and Mohawk rivers. As stated earlier, *E. b. blennioides* (the upper Ohio River subspecies) is present in the upper Genesee River, while *E. b. pholidotum* is present in the lower Genesee River. The upper and lower Genesee populations are completely separated on lateral-line scale counts (Table 2), and there are significant differences in number of dorsal soft rays and lateral blotches (Tables 6 and 8). These differences remain because the upper and lower populations are separated by a series of three cataracts in the Genesee River near Portageville, New York (Grabau, 1895). The upper Genesee River population of *E. b. blennioides* differs from the Allegheny River population (*b. blennioides*) in having higher numbers of dorsal soft rays and anal rays, undoubtedly a result of isolation and evolution of the upper Genesee form since its entry into that drainage (Tables 5–6). The lower Genesee population of *E. b. pholidotum* shows similar high anal ray counts, but the high count is uniform throughout the Wabash–Great Lakes race.

Distribution of *E. b. pholidotum* in this eastern area has occurred through a series of changes in drainage caused by the recession of the last glaciation in New York State. Fairchild (1908:1–88) thoroughly described these changes and the history of the retreating Wisconsin ice sheet in western New York. Some time before the lowest Lake Warren stage and its connection across central New York, and at the same time that the ice sheet was at about the level of Portageville in western New York, the upper Genesee River had resumed its preglacial course. It flowed northward toward present Lake Ontario and emptied into the pro-glacial Lake Belfast–Filmore. This lake was one of a series of pro-glacial lakes present during the recession of the ice sheet; each had various outlets that were determined by the elevation of the deglaciated areas. The Belfast–Filmore Lake, at an elevation of 1496 ft, had its outlet through the valley where present-day Cuba, New York is located, and emptied into the Allegheny River. Most likely, *E. b. blennioides* moved into the upper Genesee River at that time, although Fairchild (1928:141–148) indicated that the upper Genesee River had several connections with the Allegheny River System via outflow of local glacial lakes. As the glacier receded, other outlets were opened, like the Canisteo outlet into the upper Susquehanna River; but the fact that *E. blennioides* has not been reported from Canisteo Creek or the upper Susquehanna indicates that this species did not use that outlet. As the lake level dropped, the Genesee River was diverted from its preglacial course by a large moraine across the valley west of its present course (Grabau, 1895:366–368) and the series of three high falls was cut, in stages. With the cutting of the falls, *E. b. blennioides* was effectively isolated in the upper Genesee River. Further recession of the ice sheet, accompanied by lowering lake levels, opened the connection of the western New York glacial lakes with lower Lake Warren of the Huron–Erie basin. Probably around this time or during the successive series of Lakes Wayne, Grasmere, Lundy, and Algonquin stages (Hough, 1963), *pholidotum* moved across the Niagara front into western New York and into the lower Genesee River below the Portageville Falls. In successive lowerings, the Lake Hall and Vanuxem stages were created in New York, with outlets first westward and then eastward near Syracuse into the Mohawk Valley, according to recessions and readvances of the ice sheet. *E. b. pholidotum* probably entered the Seneca and Mohawk rivers during these stages. The last stage in this series of glacial events pertinent to the dispersal of *pholidotum* was the cutting of Niagara Falls and the second series of three falls on the Genesee River at present-day Rochester, New York, during the Lake Iroquois stage (Grabau, 1895:361). Once these barriers had been established, the Lake Ontario population could no longer mix with the lower Genesee population and neither population could mix with those of the Seneca and Mohawk rivers. The meristic differences among these populations can, therefore, be attributed to this isolation and subsequent evolution.

Material Examined

Detailed locality data for all specimens examined (other than types) are not presented here but can be found in Miller (1964).

Etheostoma blennioides newmanii, Cumberland race.

Cumberland River: 34 collections, 203 specimens, 23–127 mm SL. Kentucky: CU 41458, CU 41397, CU 41443, CU 37552, UMMZ 169490, UMMZ 168043, UMMZ 171551, UMMZ 175041, CU 41782, CU 23021. Tennessee: UMMZ 168266, UMMZ 125126, UMMZ 154613, UMMZ 168182, UMMZ 154590, CU 41982, UMMZ 175273, UMMZ 175241, UMMZ 175296, UMMZ 88090, UMMZ 96357, CU 37248, CU 37277, CU 21811, USNM 7063, CU 42004, TU 19490, UMMZ 174465, UMMZ 168420, UMMZ 177605, UMMZ 168290, UMMZ 175058, CU 22160, CU 23148. St. Francis River: 15 collections, 74 specimens, 25–82 mm SL. Missouri: UM 4713, INHS (uncat.) Whitewater R., 5.5 miles N of Patton, 15 April 1960, Bridges and Smith. UMMZ 139623, UM 4712, UM 4774, UM 4711, UMMZ 139472, UMMZ 139492, CU 37189, UMMZ 139503, INHS (uncat.), St. Francis R. between Fredericktown and Ironton, 25–27 Sept. 1948, Patriarche. INHS (uncat.), St. Francis R. between Fredericktown and Ironton, 25–27 April 1948, Ill. Nat. Hist. Surv. personnel. KU 6396, UMMZ 139561, KU 5754. Black River: 38 collections, 138 specimens, 24–122 mm SL. Missouri: UM 4750, UM 4621, UM 4769, CU 24258, UM 4749, UM 4733, UM 4730, UM 4773, UM 4768, UM 4720, UM 4719, UM 4715, CU 38156, UM 4747, KU 5618, UM 4772, UM 4767, UM 4748, UM 4731, UM 4714, UM 4771, KU 3399, KU 3489, UM 4732, UM 4717, UM 4716, UM 4718, KU 3337, UMMZ 102481, UMMZ 139674, UM 4770, UM 4734, UM 4735, UM 4761, UM 4764, UMMZ 139568, UM 4763, UM 4765. Upper White River: 19 collections, 149 specimens, 28–120 mm SL. Missouri: CU 32862, UM (uncat.), White R. from Goldon to 1st night camp, T22N, R25W, Sec. 22, 23, 12 Sept. 1955, Witt and Montgomery. UMMZ 152040, UMMZ 152068, UMMZ 151294, UM 4738, CU 38329, UMMZ 151039, UMMZ 151137, CU 24291, Arkansas: KU 4545, UMMZ 128699, CU 37438, CU 36433, UMMZ 123388, UMMZ 123908, UMMZ 175431, UMMZ 169914, TU 26258.

Etheostoma blennioides newmanii, Tennessee race.

Holston River: 14 collections, 112 specimens, 40–101 mm SL. Virginia: VPI 1024, CU 9973, UMMZ 96880, UMMZ 169339, CU 21015, VPI 1026, CU 38145. Tennessee: UMMZ 157516, UMMZ 159015, UMMZ 157615, UMMZ 157448, CU 24513, UMMZ 157403, UMMZ 157424. Clinch River: 8 collections, 71 specimens, 37–102 mm SL. Virginia: UMMZ 103442. Tennessee: UMMZ 158370, UMMZ 103688, CU 25616, UMMZ 113024, KU 5330, CU 30689, UMMZ 171251. Upper French Broad River: 14 collections, 28 specimens, 22–100 mm SL. North Carolina: UMMZ 155964, UMMZ 155981, USNM 40446, UMMZ 156042, UMMZ 156070, CU 10048, UMMZ 156008, CU 9980, USNM 73537, USNM 40295, CU 29441, CU 29206, UMMZ 156220, USNM 119304. Pigeon River: 2 collections, 14 specimens, 24–79 mm SL. Tennessee: UMMZ 131501, UMMZ 131298. Little Pigeon River: 14 collections, 58 specimens, 33–92 mm SL. Tennessee: USNM 190917, USNM 190626, CU 41882, CU 41337, CU 40114, CU 23457, VPI 1404, UMMZ 129328, VPI 1772, VPI 1543, VPI 1635, CU 37688, CU 41420, UMMZ 129304. Little River: 6 collections, 43 specimens, 31–102 mm SL. Tennessee: CU 41384, VPI 1535, UMMZ 96842, UMMZ 129434, USNM 190864, CU 24632. Little Tennessee River: 5 collections, 64 specimens, 35–107 mm SL. Tennessee: UMMZ 129399, UMMZ 163284, UMMZ 129472, UMMZ 112596, UMMZ 165604. Sequatchie River: 2 collections, 9 specimens, 28–63 mm SL. Tennessee: UMMZ 168147, UMMZ 168120. Elk River: 1 collection, 6 specimens, 43–73 mm SL. Tennessee: CU 24672. Duck River: 2 collections, 2 specimens, 54–70 mm SL. Tennessee: CU 37315, CU 37234. Tennessee River: 12 collections, 23 specimens, 40–92 mm SL. Georgia: UG 689, UG 281, USNM 162432, USNM 190700, USNM 70701, UG 789. Alabama: UMMZ 168545, UMMZ 177726, USNM 63126, USNM 36665, USNM 36180, UMMZ 105666.

Etheostoma blennioides newmanii, Arkansas race.

Little Red River: 6 collections, 92 specimens, 30–78 mm SL. Arkansas: UMMZ 169962, TU 22706, TU 26259, CU 41967, TU 26231, TU 26246. Arkansas River: 46 collections, 207 specimens, 24–97 mm SL. Kansas: KU 2885, KU 2238, KU 3780, KU 3588, KU 3191, KU 4364. Missouri: UMMZ 151509, UMMZ 151574, CU 42335, UM 4728. Arkansas: CU 24887, CU 35571, TU 12283, UMMZ 123841, UMMZ 128677, CU 24372, UMMZ 177211, TU 15589, UMMZ 169956, CU 42254. Oklahoma: UG 650, UMMZ 116444, UMMZ 116497, UMMZ 116775, UMMZ 103156, UMMZ 137869, KU 2415, OAM 4849, OAM 4646, OAM 4652, OAM 3155, UMMZ 116656, UMMZ 116676, UMMZ 103182, USNM 161577, CU 17888, KU 2616, UMMZ 127260, UMMZ 127311, OAM 1010, OAM 1092, OAM 1233, OAM 950, OAM 1137, UMMZ 109431, OAM 741. Ouachita River: 13 collections, 129 specimens, 28–72 mm SL. Arkansas: USNM 36418, UMMZ 170002, UMMZ 123213, KU 3526, KU 6910, USNM 165935, KU 3544, UMMZ 123066, KU 6048, TU 12296, KU 6045, USNM 165934, KU 6929. Saline River: 5 collections, 60 specimens, 24–73 mm SL. Arkansas: USNM 42729, USNM 172042, CU 42247, TU 7075, USNM 165928.

Etheostoma blennioides gutselli.

Little Tennessee River: 23 collections, 57 specimens, 24–104 mm SL. North Carolina: Paratypes—USNM 92580, USNM 197411. UMMZ 156454, UMMZ 156510, UMMZ 156469, CU 37921, UMMZ 156494, UMMZ 156577, UMMZ 156464, UMMZ 156601, UMMZ 129527, CU 24563, UMMZ 129539, UMMZ 129570, UMMZ 131233, UMMZ 163302, UG 796, UMMZ 156620. Georgia: UG 640, UG 634, UG 632, UG (uncat.), Betty's Cr. at bridge at Dillard, 9 May 1959. UG 633, UG 659, UG 314. Pigeon River: 4 collections, 27 specimens, 27–85 mm SL. North Carolina: UMMZ 131245, CU 42103, USNM 42430, CU 49738.

Etheostoma blennioides: newmanii × gutselli, Hiawassee River intergrades.

Hiawassee River: 41 collections, 103 specimens, 19–110 mm SL. North Carolina: UMMZ 156430, UMMZ 156444, UMMZ 156320, UMMZ 156332, UMMZ 156310, UMMZ 158302, UMMZ 156403, UMMZ 156415, UMMZ 156370. Georgia: CU 38101, UG 322, UG 527, UG 776, UG 748, CU 10986, CU 41466, UG 535, UG 579, UG 577, UG 470, UG 580, UG 540, UG 573, UG 172c, UG 742, UG 578, UG 760, CU 38054, CU 37885. CU 38125, CU 42169, UG 471, UG 571, UG 524, UG 775, UG 758, UG 781, UG 401, CU 41987, CU 42127. Tennessee: UMMZ 165578.

Etheostoma blennioides blennioides. Arranged from northeast to southwest along the course of the Ohio River:

Upper Genesee River: 5 collections, 53 specimens, 30–86 mm SL. New York: CU 8385, CU 29520. Pennsylvania: CU 29502, CU 20629, CU 23323. Allegheny River: 6 collections, 72 specimens, 31–70 mm SL. New York: CU 4618, CU 19941. Pennsylvania: CU 40578, CU 40781, CU 40939, CU 10708. Shenango River: 1 collection, 10 specimens, 51–75 mm SL. Pennsylvania: CU 4160. Monongahela River: 8 collections, 85 specimens, 30–72 mm SL. Pennsylvania: UMMZ 61712. West Virginia: CU 32654, USNM 196856, USNM 196855, CU 32323, USNM 196858, USNM 196857, CU 13584. Potomac River: 3 collections, 50 specimens, 45–62 mm SL. Maryland: CU 31525, CU 31519, CU 31509. Ohio River: 5 collections, 39 specimens, 20–76 mm SL. West Virginia: CU 4435, CU 5727, CU 4543, CU 13607, CU 4817. Little Kanawha River: 2 collections, 6 specimens, 36–66 mm SL. West Virginia: CU 32426, WVU 1062. New–Kanawha River: 14 collections, 165 specimens, 31–76 mm SL. North Carolina: CU 7686, CU 7699. Virginia: UMMZ 95251, CU 25306, CU 24953, UMMZ 95368, CU 8032. West Virginia: CU 14813, CU 32396, UMMZ 165689, CU 25393, UMMZ 165710, CU 5806, CU 25770. Guyandot River: 1 collection, 9 specimens, 35–53 mm SL. West Virginia: CU 14797. Big Sandy River: 2 collections, 35 specimens, 31–81 mm SL. West Virginia: CU 13431, CU 13492. Muskingum River: 5 collections, 66 specimens, 33–67 mm SL. Ohio: OSU 4-218, OSU 1297, OSU 11662, UMMZ 66897, OSU 2176. Scioto River: 6 collections, 98 specimens, 29–77 mm SL. Ohio: OSU 12716, CU 32952, OSU 2364, CU 42052, CU 42222, OSU 1337. Miami River: 5 collections, 56 specimens, 20–68 mm SL. Ohio: OSU 2298. Indiana: UMMZ 112827, UMMZ 112828, UMMZ 112826, UMMZ 112823. Little Sandy River: 2 collections, 7 specimens, 28–54 mm SL. Kentucky: CU 25581, UMMZ 126947. Tygerts Creek: 1 collection, 10 specimens, 43–58 mm SL. Kentucky: CU 24328. Licking River: 3 collections, 28 specimens, 40–73 mm SL. Kentucky: UMMZ 126948, UMMZ 171454, CU 37520. Kentucky River: 11 collections, 115 specimens, 21–76 mm SL. Kentucky: UMMZ 154471, UMMZ 177849, UMMZ 154441, CU 41365, UMMZ 168883, UMMZ 154491, UMMZ 159050, CU 25640, UMMZ 144400, UMMZ 144370, CU 37300. Harrods Creek: 2 collections, 23 specimens, 36–73 mm SL. Kentucky: UMMZ 120544, KU 4127. Salt River: 3 collections, 26 specimens, 19–82 mm SL. Kentucky: KU 5695, KU 4092, KU 6046.

Etheostoma blennioides: newmanii × blennioides.

Green River: 15 collections, 169 specimens, 20–83 mm SL. Kentucky: KU 5714, UMMZ 165429, UMMZ 178216, KU 5787, CU 37622, UMMZ 171660, UMMZ 165261, UMMZ 165341, UMMZ 154703, UMMZ 154720, UMMZ 154665, UMMZ 177807, UMMZ 178141, UMMZ 168238, UMMZ 165297.

Etheostoma blennioides pholidotum, Wabash–Great Lakes race.

Mohawk River: 1 collection, 5 specimens, 27–56 mm SL. New York: CU 7270. Seneca River: 2 collections, 15 specimens, 48–65 mm SL. New York: CU 23438, CU 23042. Lower Genesee River: 6 collections, 48 specimens, 28–70 mm SL. New York: CU 7998, CU 7581, CU 3555, CU 33151, CU 33147, CU 7097. Lake Ontario: 6 collections, 119 specimens, 33–85 mm SL. New York: UMMZ 99182, CU 22398, CU 27046, CU 5439, CU 7271, CU 33149. Lake Erie: 8 collections, 127 specimens, 29–71 mm SL. New York: CU 6897. Pennsylvania: WVU 898. Ohio: OSU 9778, KU 2795, CU 15012, OSU 4270, OSU 5304. Michigan: UMMZ 113310. Lake St. Clair: 6 collections, 58 specimens, 24–73 mm SL. Ontario: UMMZ 85561, UMMZ 85545, UMMZ 89036, UMMZ 89053, UMMZ 81257, UMMZ 85515. Detroit River: 3 collections, 40 specimens, 21–83 mm SL. Michigan: CU 41775, CU 33148, UMMZ 136903. Saginaw River: 1 collection, 19 specimens, 34–56 mm SL. Michigan: UMMZ 137163. Maumee River: 8 collections, 101 specimens, 19–81 mm SL. Michigan: UMMZ 102058. Indiana: IU 153. Ohio: OSU 1227, CU 30954, OSU 3513, OSU 11661, OSU 4166, UMMZ 107546. Wabash River: 13 collections, 186 specimens, 17–75 mm SL. Indiana: CU 1563, IU 28, UG 215, CU 32223, CU 3977, IU 113, UMMZ 99954, IU 347, IU 233, IU 20, IU 350. Illinois: CU 42251, CU 3044.

Etheostoma blennioides pholidotum, Missouri race.

Osage River: 26 collections, 157 specimens, 20–84 mm SL. Kansas: KU 3765, KU 2917, CU 42233, KU 2864, KU 3577, KU 5391. Missouri: UM 4722, UM 4758, UM 4753, UMMZ 150093, UMMZ 150949, CU 23477, KU 3490, KU 3391, UMMZ 151957, CU 37379, KU 5665, UMMZ 151918, UM 4756, UMMZ 152909, KU 5823, UMMZ 152849, UMMZ 152707, UMMZ 152803, UMMZ 152755, CU 32887. Meramec River: 11 collections, 131 specimens, 27–73 mm SL. Missouri: CU 37327, UMMZ 149579, UMMZ 149665, UMMZ 148368, CU 38151, CU 10777, INHS (uncat.) Meramec River, 10.0 miles NE of Salem, Sept. 1950. CU 34423, UMMZ 149797, UMMZ 155863, UMMZ 149742. Saline Creek: 1 collection, 5 specimens, 32–49 mm SL. Missouri: UMMZ 149828.

Etheostoma blennioides: pholidotum × newmanii, Gasconade River intergrades.

Gasconade River: 20 collections, 53 specimens, 30–81 mm SL. Missouri: KU 3488, UMMZ 152242, CU 25630, KU 3322, UM 4723, UMMZ 152216, KU 3390, UMMZ 152265, UMMZ 152483, UMMZ 152451, UMMZ 152395, UMMZ 152367, UMMZ 152878, UMMZ 151992, INHS (uncat.) Gasconade River, 1.0 mile E of Hartville, 10–13 Sept. 1950, Lowry. UMMZ 152188, CU 24308, CU 37355, UMMZ 152317, UMMZ 152294.

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Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, 75 Virginia Beach Drive, Miami, Florida 33149.

Bacteriological Study of the Natural Flora of the Eastern Oyster, *Crassostrea virginica*

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Bacteriological Study of the Natural Flora of the Eastern Oyster, *Crassostrea virginica*

Recent progress in the culture of bivalve larvae (V. L. Loosanoff and H. C. Davis, *In* "Advances in Marine Biology," **1,** 1–136, Academic Press, New York and London, 1963) has made it possible to rear economically important bivalve mollusks under controlled conditions in hatcheries. Before a study of the bacterial flora of the larvae themselves was undertaken, a study was made of the bacterial flora of the Eastern oyster, *Crassostrea virginica,* in Long Island Sound. In the past, oyster bacteriology has dealt chiefly with coliforms since their presence gives an index of fecal pollution and, therefore, is of public health significance. We are now concerned with the bacterial flora of the oyster, not in terms of its containing organisms associated with human beings, but potential pathogens of the oyster and its progeny.

The natural bacterial flora of the Pacific oyster, *Crassostrea gigas,* was determined in a study by R. R. Colwell and J. Liston (*Appl. Microbiol.,* **8,** 104–109, 1960). Our study of Eastern oysters has shown the presence of the same bacterial genera, with the exception that no gram-positive bacteria were found. Aseptically prepared oyster homogenates were inoculated on an enriched seawater agar and incubated at 18°C for 7 days. A total of 96 isolates were obtained for taxonomic and physiological study. All isolates were gram-negative, short, or pleomorphic, rods; 34 (35.4%) were pigmented (yellow or orange) and 55 (57.3%) were motile (all but one was monotrichous, polar flagellated). With the scheme of J. M. Shewan, G. Hobbs, and W. Hodgkiss (*J. Appl. Bacteriol.,* 23, 379-390, 1960) 31.2% of the isolates belonged to the genus *Pseudomonas,* 26.0% to the genera *Flavobacterium-Cytophaga,* 25.0% to the genus *Vibrio,* and 17.7% to the genera *Achromobacter–Alcaligenes.* The inability to distinguish conclusively between *Flavobacterium* and *Cytophaga* or between *Achromobacter* and *Alcaligenes* made it more realistic to pair these genera.

Physiologically the isolates were more proteolytic (87.4%) than amylolytic (49.0%) or lipolytic (70.8%). Reactions in the MOF (marine oxidation-fermentation) medium of E. Leifson (*J. Bacteriol.,* **85,** 1183–1184, 1963) showed that 35 (36.4%) of the isolates attacked glucose oxidatively and 25 (26.0%) fermentatively; 26 (27.1%) produced no reaction in the medium. Ten isolates (10.4%) did not grow in the medium, presumably because of inhibition by phenol red. Tests of the ability of the isolates to reduce nitrate to nitrite, produce ammonia from peptone, and produce indole from tryptophan showed 54 (58.1%), 40 (43.0%), and 19 (20.4%), respectively, to be active. Only 4.3% of the isolates grew in a broth medium prepared with distilled water as diluent; 41.9% grew in a basal medium consisting of seawater enriched with glucose and ammonium chloride. Disc and lawn sensitivity tests showed all isolates to be sensitive to chloramphenicol and tetracycline, where 90.4% were sensitive to penicillin, and 79.6% to streptomycin. The genera enzymically most active were *Vibrio* and *Pseudomonas* in that order. All the isolates are common inhabitants of marine waters (S. J. Altschuler and G. A. Riley, *Bull. Bingham Oceanogr. Coll.,* **19,** 81–88, 1967; J. M. Sieburth, *J. Exptl. Marine Biol. Ecol.,* **1,** 98–121, 1967; U. Simidu and K. Aiso, *Bull. Japan. Soc. Sci. Fish.*, 28, 1133–1141, 1962). Although gram-positive bacteria are usually not considered abundant in seawater, it is surprising that a sessile invertebrate, such as the oyster, does not concentrate gram-positive bacteria probably present in Long Island Sound bottom sediments. It will be of interest to learn if hatchery-reared larval and juvenile oysters harbor a bacterial flora similar to that of the adult animals from Long Island Sound.

Robert A. Murchelano
Carolyn Brown
Biological Laboratory
Bureau of Commercial Fisheries
U. S. Department of the Interior
Milford, Connecticut 06460

Received July 3, 1968

Synopsis of Biological Data on Hawaiian Species of Stolephorus

by

Eugene L. NAKAMURA
Bureau of Commercial Fisheries Biological Laboratory
Honolulu

Data on identity, distribution, bionomics and life history, population, and exploitation of the nehu (Stolephorus purpureus) are summarized. The nehu, an engraulid fish, is used as live bait in the skipjack tuna (Katsuwonus pelamis) fishery in Hawaii. Data on the identity and distribution of the roundhead (S. buccaneeri), a second Hawaiian engraulid, are also summarized. The taxonomic status of the roundhead has been questioned, since morphological intermediates between it and the nehu have been found.

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Visual Acuity of Two Tunas, *Katsuwonus pelamis* and *Euthynnus affinis*

Eugene L. Nakamura

Two tunas, *Katsuwonus pelamis* and *Euthynnus affinis*, were trained to discriminate between vertically and horizontally striped images. The striped images were projected on a plate of opal glass which rested against a window of the experimental tank. Visual acuity depended upon the width of the stripes and the distance between the fish and the window at the instant the projector was turned off. The fishes were adapted to an illumination of 170 luxes. At lower luminances of the white stripes, the visual acuities of the two species were similar. At higher luminances of the white stripes, *K. pelamis* had a greater visual acuity. Maximum visual acuity for *K. pelamis* was about 0.180 and for *E. affinis* about 0.135.

Introduction

VISUAL acuity is the ability to see clearly the fine details of objects, especially as these objects become smaller and closer together. Its measurement and attendant problems have been reviewed by Pirenne (1962) and Riggs (1965). Riggs listed four types of visual acuity: detection, recognition, localization, and resolution. He stated ". . . the task of resolution has been widely regarded since the time of Helmholtz as the most critical aspect of visual acuity." Resolution is the perception of the separate elements of an object and is the type of acuity of concern in this paper.

Few experimental measurements of visual acuity of fishes have been made. Brunner (1934) measured that of the European freshwater minnow (*Phoxinus laevis*), Yamanouchi (1956) that of the marine convictfish (*Microcanthus strigatus*), and Baerends, *et al.* (1960) that of the cichlid (*Aequidens portalegrensis*). This paper presents the measurements of the visual acuity of two scombrids, skipjack tuna (*Katsuwonus pelamis*) and little tunny (*Euthynnus affinis*). These measurements are believed to be the first for pelagic marine fishes.

Tank and Apparatus

Visual acuity was measured in a U-shaped tank 15.9 m long, 4.9 m wide, and 1.2 m deep (Fig. 1). The arms of the tank were 1.8 m wide. During an experiment only one arm of the tank was used. The other was sealed off with a partition.

The tank was enclosed within a Quonset hut. The inside walls of the building were painted with non-reflecting black paint. Two rows of fluorescent lights (Westinghouse Cool White[1]), one over the center of each arm of the tank, ran the length of the building. For spectral emission of these lights, see Withrow and Withrow (1956:180, figs. 3–15).

At the end of each arm of the tank was a clear glass window against which an opal glass plate was placed. Striped images were focused upon this plate with a projector. The window was masked so that the image was focused within a 27.9-cm square.

The experiments were conducted from one of the observation booths above the end of each arm. Observations were made through a slit. Three control buttons were located in the booth: one to operate the projector, a second to operate the slide changer, and a third to operate the shocking apparatus. A feeding tube extended from the booth so that food could be dropped without the observer being seen. Copper electrodes were suspended next to the walls of the tank. Salt water from a well was aerated before it flowed into the tank (Nakamura, 1964; Strasburg, 1964).

Test slides of black and white stripes of equal width were made by drawing stripes with India ink on drawing paper and photographing the stripes with high-contrast film. Exposures were made at various distances from the drawing so that various numbers of stripes were obtained within a 3.8-cm square on the negative. The negatives were then cut and sealed in square cardboard mounts. The alternating stripes varied from 3 black and 4 white to 10 black and 11 white

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[1] Trade names mentioned in this publication do not imply endorsement of products.

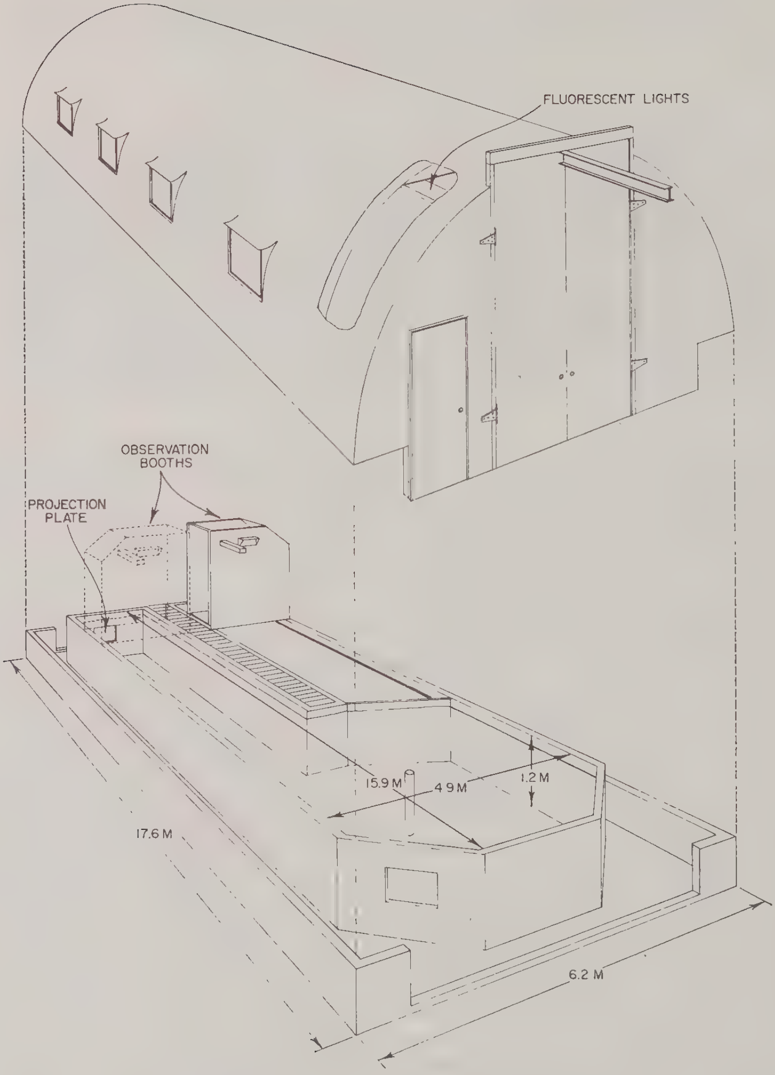

Fig. 1. Diagram of experimental tank.

(Fig. 2). All slides were made with white stripes on the outer sides so that the projected image on the opal plate was square. Several slides of each series of stripes were made and placed in slide trays so that the stripes were alternately vertical and horizontal. Thus, to change from vertical to horizontal stripes, the slide-changer button was pressed. To change stripe size, the slide tray was changed. Neutral-density gelatin filters were used to decrease the intensity of the light from the projector.

TRAINING AND EXPERIMENTAL PROCEDURES

The fish were trained to discriminate between vertically and horizontally striped images. Food and electric shock were used as reinforcement. A single fish was used during each experiment. Training was conducted about an hour once every day. Usually, fish learned to perform in the desired manner (10% or less errors) within one week of training.

A fish spent most of its time in the large part of the tank opposite the observation

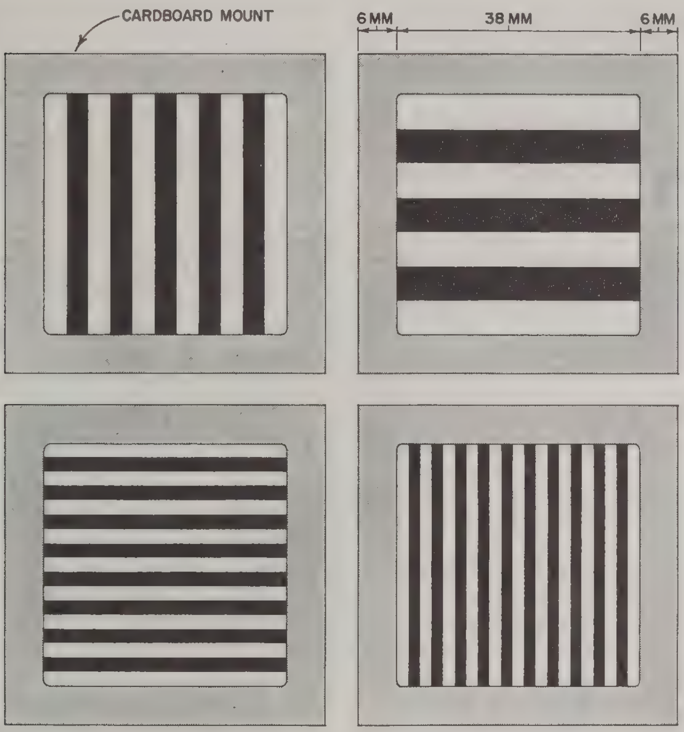

Fig. 2. Examples of test slides.

booth (Fig. 1). Training was started by introducing food (fish) in the arm of the tank. Each delivery of food was preceded by a projection of vertical stripes on the opal plate at the window under the booth. The fish soon learned to swim toward the food-drop area when the projector light was turned on.

After this training period both vertical and horizontal stripes were presented. The projector was turned on when the fish was at the end of the tank opposite the observation booth and turned off when the fish reached a selected distance from the window. After projection of vertical stripes, food was dropped from the feeding tube; after projection of horizontal stripes the fish received an electric shock if it passed between the electrodes, which it had to do to reach the food-drop area. This procedure was continued until the fish learned to swim to the food-drop area when vertical stripes had been presented and to turn around before reaching the electrodes when horizontal stripes had been presented.

Experiments were conducted as follows. The projector was turned on when the fish was at the end of the tank opposite the booth. The fish reacted by swimming toward the light. When the fish reached a selected distance, which was marked with a bar across the floor of the tank, the projector was turned off. If the fish erred by continuing down the tank when the stripes were horizontal, it received a shock. If it erred by turning around when the stripes were vertical, it received no food. In each trial 10 vertically and 10 horizontally striped images were presented in a random sequence. The first trial was conducted without filters. In the next trial the luminance of the white stripes was reduced by placing a neutral-density gelatin filter ahead of the lens of the projector. The luminance was reduced progressively in subsequent trials until the fish made 10 or more errors. At this point, the luminance of the white stripes by which the fish discriminates between the vertical and horizontal stripes was assumed to be subliminal. This end point was always con-

TABLE 1. TEST RESULTS WITH SKIPJACK TUNA (*Katsuwonus pelamis*) No. 2, 47.3 CM FORK LENGTH. Ten vertically and 10 horizontally striped images in a random sequence were presented at each of the progressively lower luminances. Test slides: nine black and 10 white stripes. Distance between window and crossbar: 6 m. Visual angle: 8.59 min.

Luminance of White Stripes at Window (ft-Lamberts)	Errors			
	Vertical Stripes	Horizontal Stripes	Total	%
>100.0	0	1	1	5
42.0	0	2	2	10
11.0	0	0	0	0
3.0	0	1	1	5
0.796	0	3	3	15
0.361	1	5	6	30
0.213	0	5	5	25
0.163	1	10	11	55
0.126	2	9	11	55

TABLE 2. TEST RESULTS WITH LITTLE TUNNY (*Euthynnus affinis*) No. 1, 36.4 CM FORK LENGTH. Ten vertically and 10 horizontally striped images in a random sequence were presented at each of the progressively lower luminances. Test slides: three black and four white stripes. Distance between window and crossbar: 3 m. Visual angle: 44.68 min.

Luminance of White Stripes at Window (ft-Lamberts)	Errors			
	Vertical Stripes	Horizontal Stripes	Total	%
>100.0	0	1	1	5
0.796	0	2	2	10
0.213	1	4	5	25
0.096	0	7	7	35
0.057	0	6	6	30
0.044	0	5	5	25
0.034	0	5	5	25
0.026	0	2	2	10
0.020	4	5	9	45
0.015	3	5	8	40
0.012	1	10	11	55
0.009	1	10	11	55

firmed by adding another filter and determining if the fish committed 50% or more errors again. If so, the experiment was terminated for the day. Either the distance between the crossbar and the window, which ranged from three to eight m, or the set of slides was changed for the next experiment.

All experiments were conducted between 1130 and 1630 hrs. Water temperatures varied between 22.2° and 23.6° C. Illumination at mid-depth (0.5 m) of the water was 170 luxes at all times.

When the luminance of the white stripes was near threshold for stripe discrimination, food as a reward was apparently a greater incentive than shock as a deterrent, for the fish often continued toward the window, and into the electrode area when horizontal stripes were presented. Examples of test results are shown in Tables 1 and 2 for skipjack tuna and little tunny, respectively.

A change in the swimming behavior of a fish was evident when it began to err 50% of the time. With the white stripes at high luminances, a fish swam fast and showed no hesitation in reacting. At low luminances, when it began to err 50% of the time, a fish swam slower, and when the projector light was turned off, it hesitated before proceeding slowly down the tank.

Some imprecision was unavoidable in extinguishing the light from the projector just as the fish reached the bar across the bottom of the tank. Several measurements of the position of the fish's head when the light was turned off showed it to be within 15 cm of either side of the bar.

Luminance (photometric brightness) of the white stripes was measured with a light meter (Weston Master V) calibrated in ft-lamberts. The light meter was encased in a watertight plastic bag, taken underwater, and placed against the glass window, where the measurement was taken.

CALCULATION OF VISUAL ACUITY AND LUMINANCE

Visual acuity is, by definition, the reciprocal of the visual angle. Visual angle, measured in minutes of arc, is the angle subtended at the eye by the size of the viewed object.

Visual acuity was calculated as follows. One-half of the width of the stripes was divided by the distance between the crossbar and the window (the distance between the eyes of the fish and the stripes on the opal plate). The quotient, which equaled the tangent of one-half of the visual angle, was converted to minutes of arc. The reciprocal of twice the minutes of arc gave visual acuity.

The luminance of the white stripes was reduced by the column of water between the opal plate and the eyes of the fish. To measure this reduction, the volume attenuation coefficient was determined. This coefficient, alpha, which is an index of water clarity, is equal to the sum of the coefficients for absorption of light and for scattering of light.

Alpha was measured as follows. Photographs of one of the striped images were taken underwater in the tank from various distances. These photographs were taken with 35-mm film (Kodak Plus-X) through a yellow gelatin filter (Kodak, No. 8, K2). The film was developed and examined with a densitometer. The attenuation of the apparent brightness (ft-lamberts) of the white stripes with distance (m) was exponential as defined by the equation expressed below. The ratio of the brightnesses at an interval of one m was located in a table of exponential functions to obtain alpha. Alpha was 0.18 natural log/m. It was measured only once under the assumption that the turbidity of the water was constant throughout the experimental period.

The fish were able to distinguish stripes at luminances below the calibrated values of the light meter. To determine these lower luminances, a negatively exponential formula was first calculated with the measurable luminances and their respective filter densities, and then the appropriate extrapolations were made. Recalculations were made whenever different bulbs or different projectors were used.

The luminance of the stripes at the distance of the crossbar was calculated by:

$$B_d = B_o e^{-ad}$$

where B_d = luminance of the white stripes in ft-lamberts at the crossbar, B_o = luminance of the white stripes in ft-lamberts at the windowpane, α = volume attenuation coefficient, and d = distance between crossbar and window in meters.

EXPERIMENTAL RESULTS

Data were obtained from experiments with two skipjack tuna and two little tunny. Fork lengths of the skipjack tuna were 40.8 and 47.3 cm (weights were 1.4 and 2.0 kg, respectively); those of the little tunny were 36.4 and 43.4 cm (weights were 0.9 and 1.6 kg, respectively).

At lower luminances of the white stripes, the visual acuities of the two species were similar (Fig. 3). At higher luminances, the skipjack tuna had a greater visual acuity. The maximum visual acuity obtained for skipjack tuna was about 0.180 and for little tunny about 0.135.

COMPARATIVE VISUAL ACUITIES

Discrimination of striped images was involved in earlier works on fishes also. Brunner (1934) trained *Phoxinus laevis* to discriminate between a vertically striped square and a gray square, as did Baerends *et al.* (1960) with *Aequidens portalegrensis.* Yamanouchi (1956) trained *Microcanthus strigatus* to discriminate between vertically and horizontally striped squares. These authors used small aquaria. Brunner had a fixed distance at which the minnow had to make a choice. Yamanouchi measured the distance at which convictfish dashed toward the correct square. Baerends *et al.* did not measure visual acuity at various light intensities as the others did, but rather, visual acuity of fish of various sizes under the same test conditions.

Brunner and Yamanouchi did not calculate visual acuity. Using their data, I calculated visual acuities for the two species and plotted them against the illumination to which they were adapted (Fig. 4). The maximum visual acuity (0.200) for the convictfish was more than twice that (0.093) for the minnow.

Since visual acuity is affected by the light adaptation of the eye, the data for the convictfish and minnow were compared with those of the scombrids at an illumination of 170 luxes, the illumination to which the scombrids were adapted. At this illumination, the visual acuities of the four species were: *Katsuwonus pelamis* 0.180, *Microcanthus strigatus* 0.160, *Euthynnus affinis* 0.135, and *Phoxinus laevis* 0.093.

Data on spacing of cones in the retina also have been used to measure visual acuity. The assumption that visual acuity in fishes is dependent upon cone density has been questioned, however, by O'Connell (1963). He and others have found a negative regression between cone density and lens diameter. The decrease in density with larger eyes did not compensate for the expansion of the image area on the basis of Matthiessen's ratio (distance from lens center to retina equals 2.55 × lens radius). O'Connell

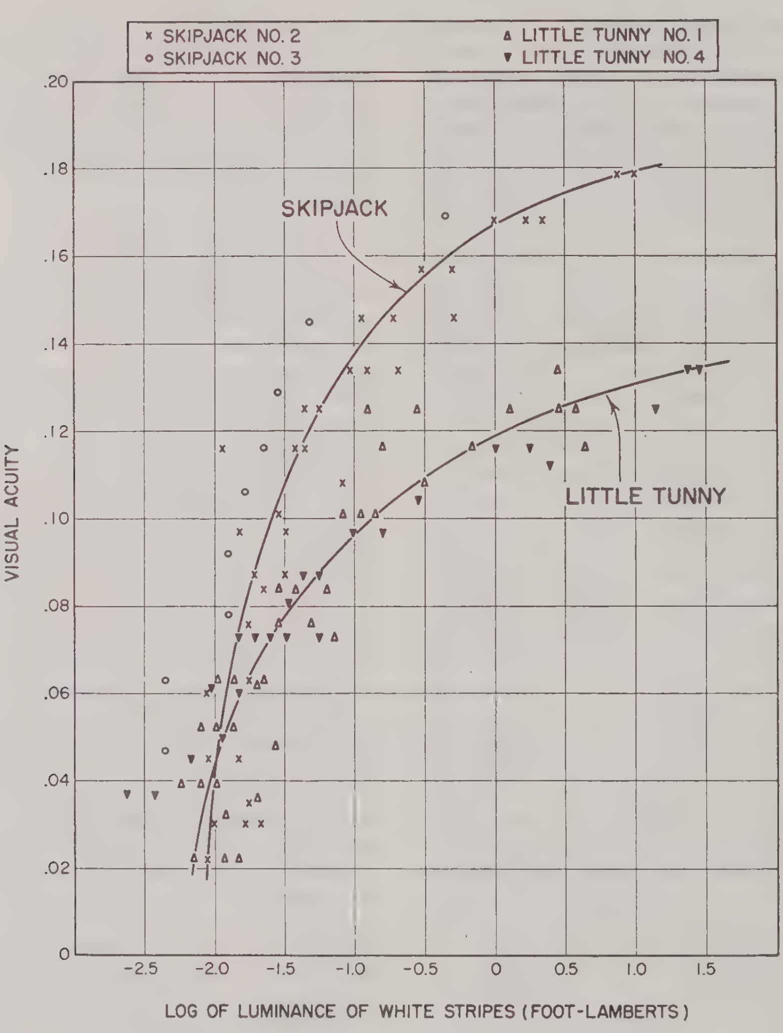

Fig. 3. Visual acuity curves of skipjack tuna (*Katsuwonus pelamis*) and little tunny (*Euthynnus affinis*) at adaptive illumination of 170 luxes. Curves fitted by eye.

concluded that either proportions of the eye cannot be used for determining the image area on the retina or that visual acuity varies with fish size. Baerends *et al.* (1960) have shown experimentally that visual acuity does change with size of fish.

The smallest visual angle (minimum separable angle) calculated from the diameter of a foveal cone in the retina of man has been greater than the smallest visual angle obtained experimentally (citations in Polyak, 1941). In fish the smallest visual angle determined by the diameter of a cone has been less than that obtained experimentally.

Yamanouchi (1956) determined the distribution of cones in the retina of the convictfish and then calculated the minimum separable angle, assuming that resolving power depends on the stimulation of adjacent cones. This angle (3.60 min) was smaller than that obtained experimentally (4.98 min). He used averaged data for fish ranging from 9 to 11 cm long.

The minimum separable angle for skipjack tuna has been calculated by Tamura and Wisby (1963) who based their calculation on the assumption that resolution depended upon the stimulation of cones sepa-

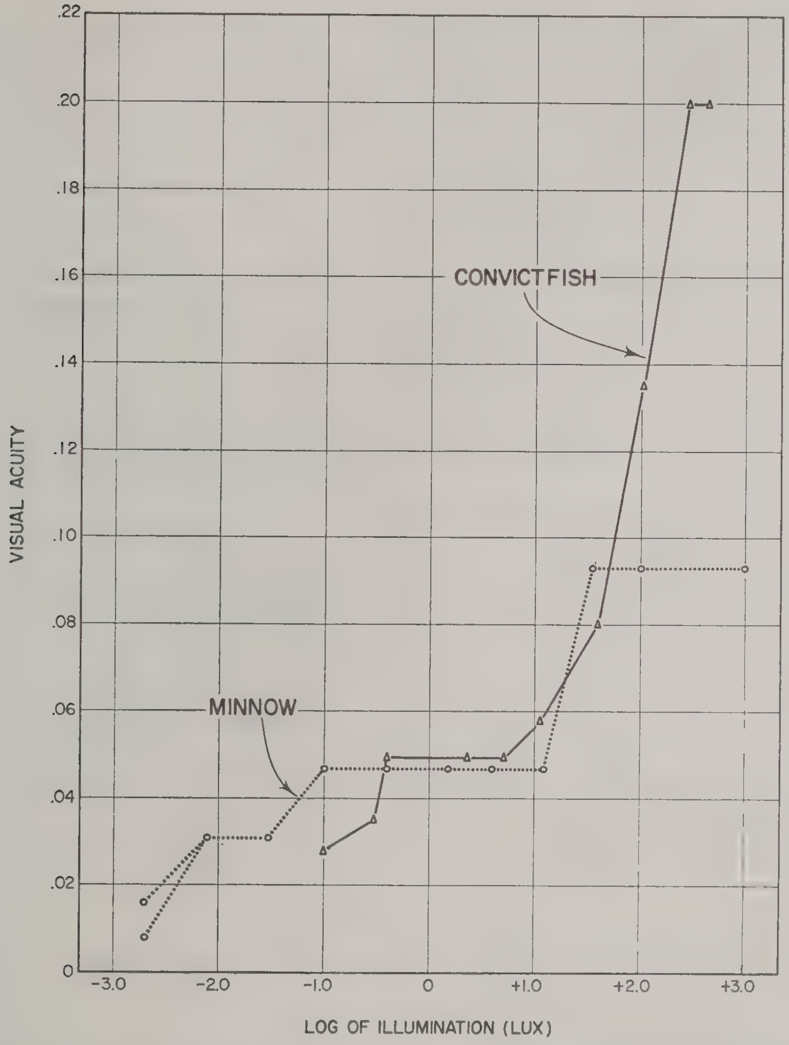

Fig. 4. Visual acuity curves of the convictfish (*Microcanthus strigatus*) and the European minnow (*Phoxinus laevis*). (Adapted from data of Brunner (1934) and Yamanouchi (1956).)

rated by at least one unstimulated cone. This angle (2.3 min) was less than that (5.6 min) obtained experimentally by me. When the minimum angle was recalculated from the density of cones in the temporal region of the retina (they used the density in the ventral portion of the retina; see Tamura and Wisby, 1963:table 4), the retinal region most probably used by skipjack tuna in my experiments, the angle (4.3 min) was still smaller than that obtained experimentally. The standard length of the skipjack tuna used by Tamura and Wisby was 52 cm.

SIGNIFICANCE OF VISUAL ACUITY TO SCOMBRIDS

The role of visual acuity in the life of pelagic fishes may involve, in addition to the detection of prey and predators, the recognition of transient and permanent body marks. Skipjack tuna and other pelagic fishes exhibit transient color markings at certain times, such as during feeding (Nakamura, 1962; Nakamura and Magnuson, 1965; Strasburg and Marr, 1961) or during courtship (Magnuson and Prescott, 1966). These markings may convey information about the presence of food to other fish in the school, or signal aggressive intentions. Visual recognition of certain permanent body marks may aid a fish to distinguish its own kind from others closely resembling it (Nakamura and Magnuson, 1965).

Maximum distances of resolution of prey or body marks can be determined by reversing the calculations for visual acuity. These distances would pertain if the fish were in waters with the same visibility conditions as in the experimental tank. With an unobscured sun at an altitude of 65° so that the illumination at the surface of the sea was 107,600 luxes (Duntley, 1960), and with an alpha of 0.18 natural log/m, an illumination of 170 luxes (the same as in the tank) would be at 36 m.

The mean gap between gill rakers of the first arch of a skipjack tuna 40.8 cm long (size of the smaller skipjack tuna used in my work) is 0.9 mm. This fish could thus take a particle wider than 0.9 mm into its mouth and not lose it through its branchial apparatus. If it were to prey upon an organism 0.9 mm wide in waters with visibility conditions mentioned above, it would be able to resolve the prey at a maximum distance of 54 cm. Similarly, the mean gap between gill rakers of the first arch for a little tunny 36.4 cm long is 1.4 mm. The little tunny would be able to resolve a particle this wide at a maximum distance of 67 cm.

Transient vertical bars on the flanks of a skipjack tuna may be two cm wide. Another skipjack tuna would be able to resolve this mark from a maximum distance of 12.4 m under the visibility conditions described above. Similar transient bars on the flanks of a little tunny would be visible to another little tunny at a maximum distance of 9.3 m.

Permanent black stripes are on the ventrolateral surfaces of skipjack tuna and on the posterior half of the dorsal and dorsolateral surfaces of little tunny. These stripes, which may be used as recognition marks, may be 0.5 cm wide. They would be resolvable at maximum distances of 3.1 m by skipjack tuna and 2.3 m by little tunny under the same visibility conditions.

Sighting distances in the sea depend to a great extent upon the brightness of an object and the brightness of its background. The size of an object may be of little consequence if this contrast in brightness is slight (Duntley, 1963; Hester and Taylor, 1965). The above calculations were made with the assumption that contrast was sufficient for visual detection.

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U. S. BUREAU OF COMMERCIAL FISHERIES BIOLOGICAL LABORATORY, HONOLULU, HAWAII 96812.

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AN APPLICATION OF THE VIRTUAL POPULATION TECHNIQUE TO PENAEID SHRIMP[1]

Richard A. Neal
Bureau of Commercial Fisheries
Biological Laboratory, Galveston, Texas 77550

ABSTRACT

Commercial catch statistics for brown shrimp (*Penaeus aztecus* Ives) from a restricted area along the Texas coast were examined by using the virtual population technique. The sum of all catches from a single year class was used as a minimum estimate of population size at the time of recruitment. The conversion of catches from pounds to numbers also made possible maximum estimates of the exploitation rate for all periods after recruitment. Monthly catches of shrimp of each size group were compared for the years 1961-66, and weights were converted to value by using the mean price per pound for each size group for the period.

Comparisons of the percentage of a year class harvested at each size with the percentage of the gross value contributed by each size group may aid in making decisions concerning the management of shrimp stocks.

INTRODUCTION

An important objective of fish and shellfish population studies is to determine the size at which individuals should be caught to provide maximum yields. Techniques commonly used to estimate optimum size at harvest require detailed knowledge of growth and mortality rates. When such information is not available, preliminary assessments of optimum size can be made from landing statistics, provided that these reflect the age or size composition of catches. The virtual population technique (Fry, 1949) is used in the following discussion to compare size composition of harvests of brown shrimp (*Penaeus aztecus* Ives) from Texas waters and to estimate maximum rates of exploitation. Relations between size at harvest and value of landings are also examined.

THE VIRTUAL POPULATION TECHNIQUE

A virtual population is defined as the number of individuals in a stock at a given time that will be caught later by the fishery (Fry, 1949). The sum of catches from a year class is an estimate of the virtual population at the time the year class became vulnerable to the fishery. It differs from the actual population size by the number of individuals that die from natural causes. Hence, the lower the rate of natural mortality, the closer the virtual population is to the actual population.

Use of this technique necessitates several assumptions. The population being studied must be well defined or, if the population is mobile, movement into the population must equal emigration from the population. Landing statistics must reflect accurately the size composition and magnitude of catches. Catches from each year class must be recognized. If the technique is used for shrimp population studies based on commercial landings, grading methods must be uniform throughout the study area.

When the catches contributing to the virtual population for a year class are considered by time periods, rates of exploitation can be calculated. The number caught during a given period divided by the number in the virtual population at the beginning of the interval is a maximum estimate of the rate of exploitation for that period. Estimates of exploitation rates are maximal because the virtual population is a minimum estimate of the actual population.

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[1] Contribution No. 255 from the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

APPLICATION OF THE TECHNIQUE TO A SHRIMP POPULATION

Shrimp landing statistics gathered by the Bureau of Commercial Fisheries and published monthly in *Gulf Coast Shrimp Data* provide information suitable for estimating virtual populations of shrimp in relatively small areas of the Gulf of Mexico. These data are tabulated according to species, weight, and size of shrimp landed, as well as by water depths and areas from which catches were made. The purpose of this paper is to demonstrate an application of the virtual population technique in which these landing statistics are used. Landings of brown shrimp (*Penaeus aztecus* Ives) from statistical areas 18 and 19 (Fig. 1) were used in the calculations for the following example. Catches of bait shrimp from bay systems adjacent to areas 18 and 19 were also included. Estimates of bait catches in the Galveston Bay system were made from the results of a survey of bait landings (Berry and Baxter, 1967), and those from Matagorda Bay were based on the number of boats operating each year.

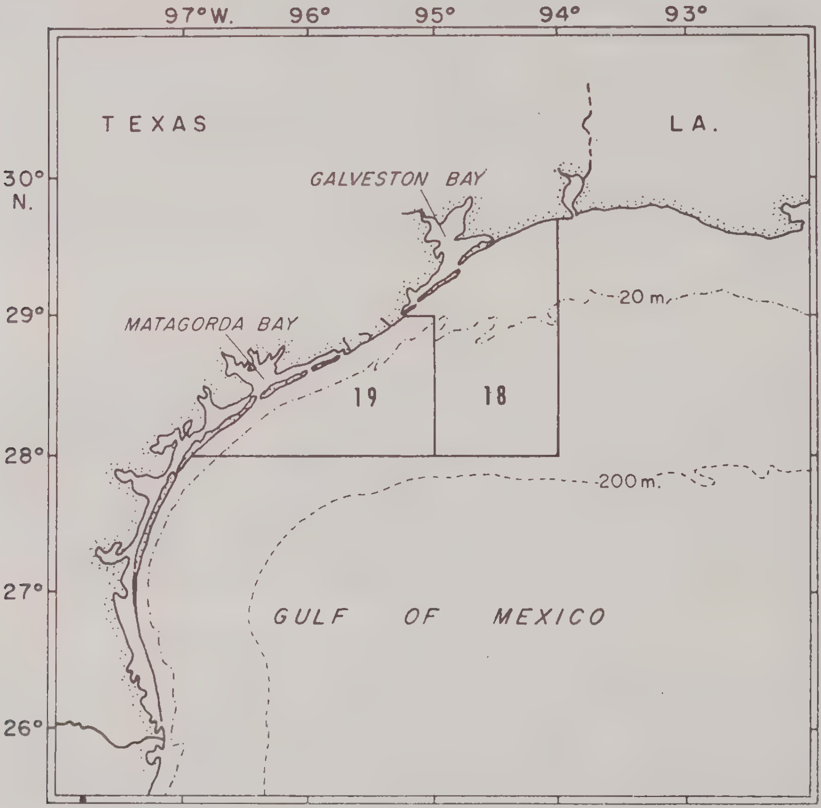
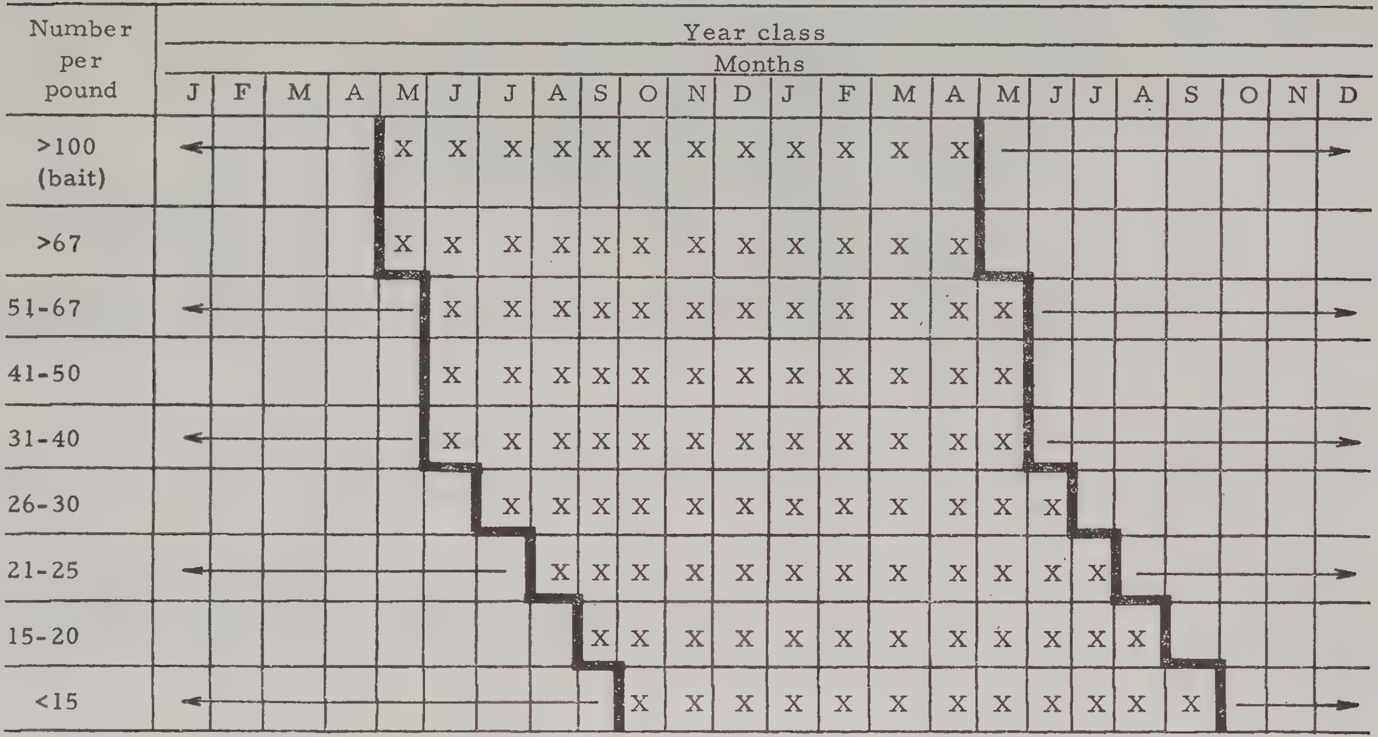


Figure 1 — Area of the Texas coast from which brown shrimp landings were tabulated (Kutkuhn, 1962).

The total weight of shrimp landed in each size group (number of headless shrimp per pound) from May 1961 through September 1966 was arranged in tabular form by months. The arrangement of the data is represented schematically in Figure 2. Landings in pounds were then multiplied by the midpoint of each size group to obtain numbers of shrimp landed.

Figure 2. Schematic representation of the arrangement of landings data.

Heavy lines are divisions between year classes.



Number per pound	Year class																						
	Months																						
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
>100 (bait)	←				X	X	X	X	X	X	X	X	X	X	X	X							→
>67					X	X	X	X	X	X	X	X	X	X	X	X							
51-67	←					X	X	X	X	X	X	X	X	X	X	X	X						→
41-50						X	X	X	X	X	X	X	X	X	X	X	X						
31-40	←					X	X	X	X	X	X	X	X	X	X	X	X						→
26-30							X	X	X	X	X	X	X	X	X	X	X	X					
21-25	←							X	X	X	X	X	X	X	X	X	X	X	X				→
15-20									X	X	X	X	X	X	X	X	X	X	X	X			
<15	←									X	X	X	X	X	X	X	X	X	X	X	X		→

TABLE 1 — THOUSANDS OF SHRIMP FROM THE 1964 YEAR CLASS TAKEN BY COMMERCIAL FISHERIES FROM STATISTICAL AREAS 18 AND 19 (SEE FIGURE 1).

No./lb. (Heads-off)	1964								1965									
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Total
> 100 (Bait fishery)	17,079	25,346	14,407	1,817	3,151	2,193	450	46	..	..	..	..	..	..	..	..	..	64,489
> 67	11,185	23,902	4,630	282	148	149	1,225	..	..	..	..	..	..	..	..	..	..	41,521
51-67	..	6,518	7,901	2,704	1,256	47	38	28	4	56	28	1	88	..	..	..	..	18,669
41-50	..	6,482	27,287	4,828	2,415	223	78	31	38	32	9	18	313	..	..	..	..	41,754
31-40	..	3,668	60,317	35,473	8,244	1,054	253	342	255	245	175	167	233	..	..	..	..	110,426
26-30	..	..	3,935	40,821	17,126	1,304	402	1,055	464	472	239	1,135	170	1,074	..	..	..	68,197
21-25	..	..	..	13,510	31,575	8,975	1,859	1,286	1,339	175	120	1,028	726	684	1,322	..	..	62,599
15-20	..	..	..	..	8,026	11,724	4,449	1,694	2,642	701	297	999	1,200	989	805	1,349	..	34,875
< 15	..	..	..	..	..	288	186	25	26	4	1	39	75	214	358	316	489	2,021
Total	28,264	65,916	118,477	99,435	71,941	25,957	8,940	4,507	4,768	1,685	869	3,387	2,805	2,961	2,485	1,665	489	444,551

Shrimp entering the fishery between May and April (entries during January through April were negligible) of each year were designated as a year class. These shrimp contributed to the commercial catch through the following September. For the years 1961-65, year classes were separated in the commercial landings statistics on the basis of changes in the number of shrimp landed in each size group. In most cases a marked decline in landings in each size group occurred between year classes. The division of year classes was made between the same months of each year (indicated by the heavy lines in Figure 2). Landings from the 1964 year class are presented in Table 1 as an example. The sum of the landings from a year class is the virtual population estimate for that year class.

The relation between shrimp size and value was also considered because the price per pound paid for shrimp increases with shrimp weight (Fig. 3). The relative value of landings in each size group by year classes was calculated from average price data for the period 1961-66. This average price was used for all years so that the value of landings could be compared directly.

A summary of virtual population estimates, relative values of the year classes, and average size at harvest by year class is presented in Table 2. The relative value of a year class is related closely to the average size at harvest.

TABLE 2 — ESTIMATES OF VIRTUAL POPULATION, RELATIVE VALUE, AND AVERAGE SIZE AT HARVEST FOR FIVE YEAR CLASSES OF BROWN SHRIMP.

(The numbers in parentheses are exclusive of bait shrimp catches.)

Year class	Virtual population (thousands of shrimp)	Relative value (thousands of dollars)	Average size (no./lb.)	Relative value per 1,000 shrimp (dollars)
1961	338,437 (230,469)	5,200 (4,300)	61.2 (38.4)	15.36 (18.66)
1962	481,238 (365,455)	7,900 (6,900)	58.7 (42.6)	16.42 (18.88)
1963	636,443 (529,786)	12,400 (11,600)	47.8 (35.3)	19.48 (21.90)
1964	444,551 (380,062)	8,900 (8,400)	47.6 (37.0)	20.02 (22.10)
1965	814,684 (692,944)	13,800 (12,800)	51.4 (41.2)	16.94 (18.47)

Rates of exploitation calculated for the period of time that shrimp were in each size category are presented in Table 3. Estimates for large shrimp (i.e., < 15, 15-20) are too high, however, because no information

TABLE 3 — MAXIMUM ESTIMATES OF RATE OF EXPLOITATION FOR EACH SIZE GROUP OF BROWN SHRIMP, BY YEAR CLASSES.

Size group	Year class 1961	1962	1963	1964	1965
> 100	0.319	0.241	0.168	0.145	0.149
> 67	0.074	0.218	0.051	0.109	0.148
51-67	0.060	0.072	0.076	0.055	0.124
41-50	0.194	0.211	0.105	0.130	0.164
31-40	0.621	0.358	0.478	0.397	0.432
26-30	0.492	0.287	0.418	0.407	0.417
21-25	0.390	0.618	0.522	0.629	0.724

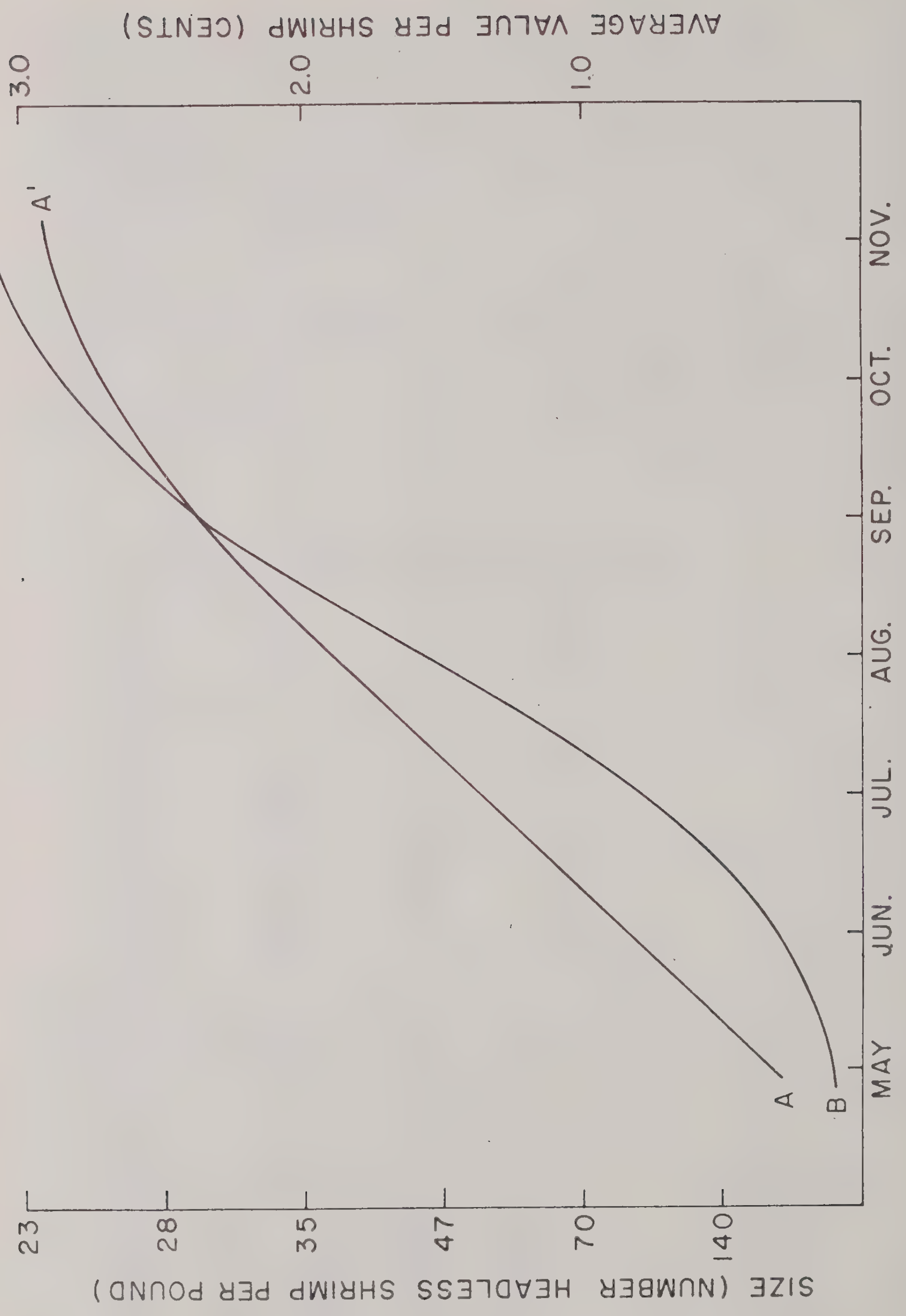


Figure 3 — Approximate growth in weight (A-A′) and corresponding increase in value (B-B′) of brown shrimp entering the fishery in May. Value was calculated from average exvessel prices in 1961-66, excluding bait shrimp.

is available on the number of shrimp that escape capture at large sizes (less than 15 to the pound). Estimates which are most seriously biased were omitted from Table 3. The average time required for a shrimp to pass through each size group was calculated by using a hypothetical growth curve for brown shrimp—length at time $t = 190\ (1 - e^{.07\,(t - t_0)})$. Exploitation rates were then converted to a weekly basis (Table 4).

TABLE 4 — MAXIMUM RATE OF EXPLOITATION PER WEEK (PERCENTAGE) BY SIZE GROUP.

Size group	Year class				
	1961	1962	1963	1964	1965
51-67	2	3	4	2	6
41-50	10	10	5	6	8
31-40	27	14	19	17	17
26-30	22	12	18	17	18
21-25	5	9	7	9	11

DISCUSSION OF RESULTS

An advantage of the virtual population technique is that it gives us an estimate of the size of an entire year class. These estimates are particularly useful as a basis for percentage comparisons. By using comparisons of the percentage of the virtual population harvested at different times and sizes, we can obtain information regarding the relation between time of harvest and size at harvest, and the relation between size at harvest and value.

The percentage of the virtual population that was captured each month is recorded for each year class in Figure 4. Most shrimp taken from each year class were caught during the first 4 or 5 months after they entered the fishery. Also, the proportion harvested each month after December was consistently small. The distribution of landings was similar from year to year, but small changes in the timing of harvests made appreciable differences in the weight of the catch.

Expressing the landing data as a percentage of the virtual population is also convenient for comparing the size distribution of landings among years. From the shrimp landings the percentage of the virtual population taken from each size category was calculated for each year class. Catch data for the 1962 and 1963 year classes are compared in Figure 5 to illustrate annual differences in sizes harvested.

Relative values of landings in each size group are presented as percentages of the total gross value for the 1962 and 1963 year classes in Figure 5.

The comparison between the 1962 and 1963 year classes illustrates possible applications of these calculations. The number of shrimp caught from the 1963 year class was 32 percent larger than the number caught from the 1962 year class (Table 2). Accompanying this 32 percent increase in catch was a 57 percent increase in relative value. Value increased almost $2 million more than would be expected from the increase in numbers of shrimp alone. Much of the 1962 catch was taken from the smaller size groups and contributed only a small proportion of the income from that year class (Fig. 5). In contrast, the numbers of the 1963 year class harvested from the 15-20, 26-30, and 31-40 size groups contributed a large proportion of the value of that year class. As a result of the differences in sizes harvested, the value per 1,000 shrimp was considerably higher in 1963 than in 1962 (Table 2).

The virtual population technique permits an investigator to examine the size composition and seasonal distribution of landings from a year class. A change in the size of shrimp harvested is frequently a goal of regulatory measures. This method of examining catches may be useful in evaluating such regulations. Maximum rates of exploitation are a basis for evaluating rates calculated by other methods.

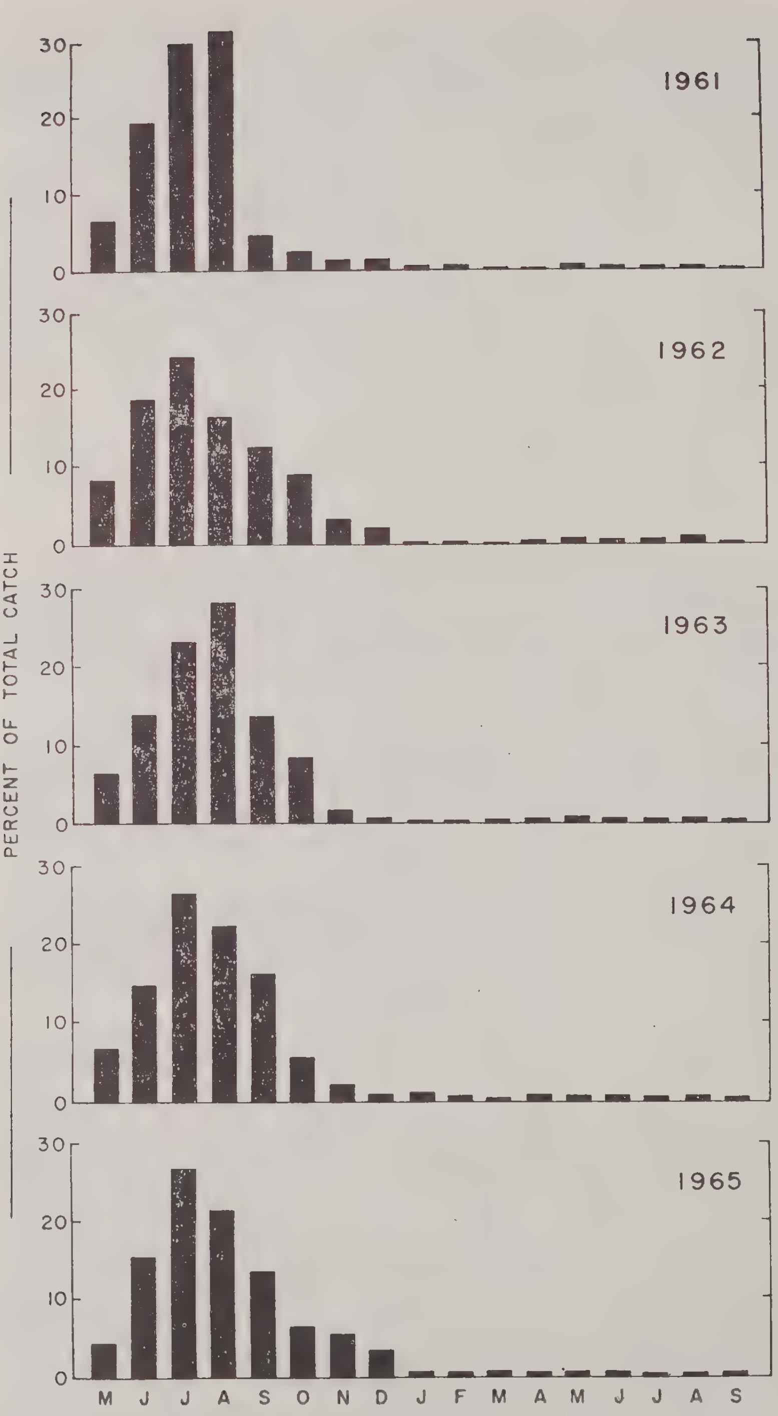


Figure 4 — Percentage of total catch in numbers of shrimp taken each month, by year classes.

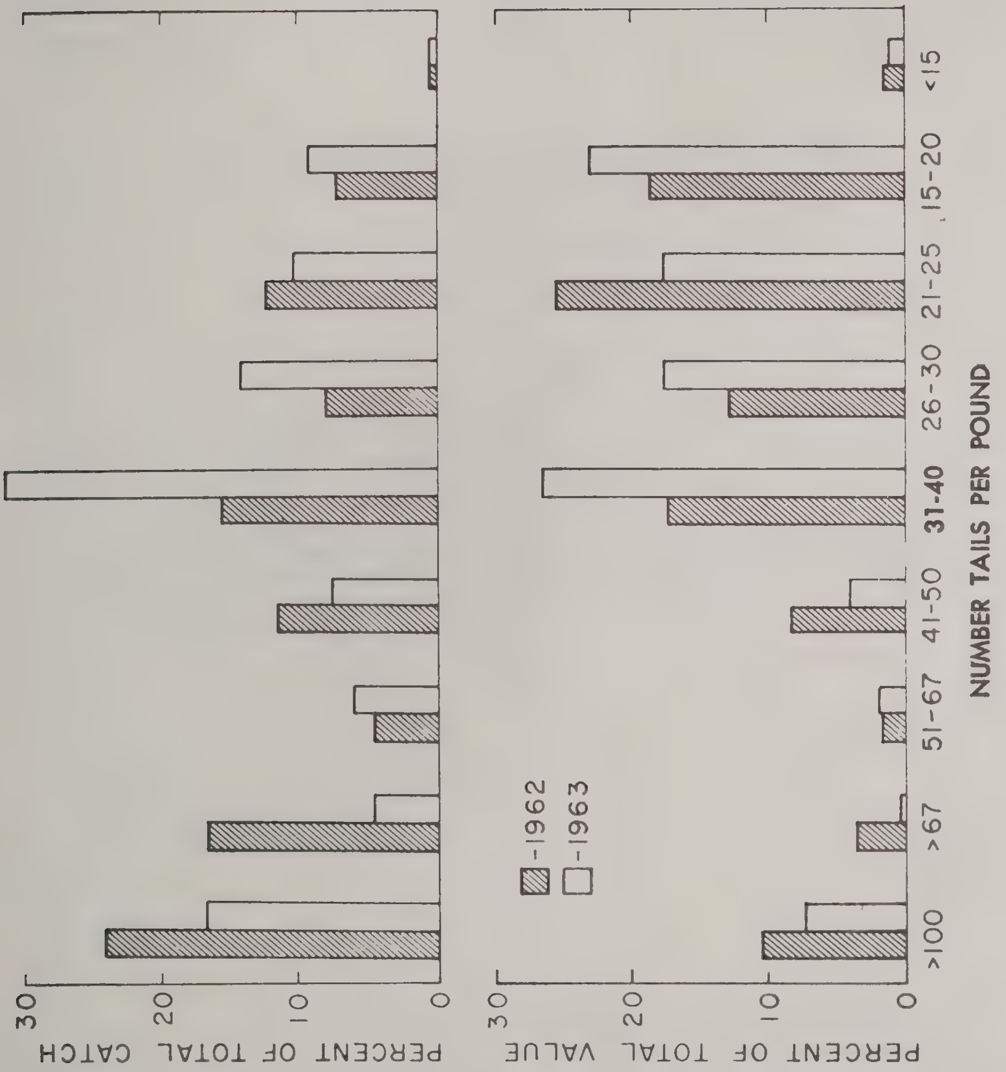


Figure 5 — Percentage of total catch in numbers of shrimp and relative value by size groups for 1962 and 1963 year classes (value based on average exvessel prices, 1961-66).

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Redescription of *Bellottia apoda* Giglioli, 1883 (Pisces, Ophidioidea)

By JØRGEN G. NIELSEN
Zoological Museum, Copenhagen
AND
DANIEL M. COHEN
Bureau of Commercial Fisheries, Washington, D.C.

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The Mediterranean ophidioid fish genus *Bellottia* is diagnosed, and its relationships with other viviparous ophidioids are discussed. Its closest relative may be *Microbrotula* Gosline. Previous opinions about *Bellottia* are summarized. A description is presented of *B. apoda*, the only known species in the genus.

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INTRODUCTION

The status of the rare and little-known Mediterranean ophidioid fish *Bellottia apoda* has long been a subject for conjecture. During the course of studies on the relationships of ophidioid genera we found it necessary to consider *Bellottia* because of its varied history in the literature. A redescription of the fish along with a review of earlier opinions of its relationships and our own conclusions are presented in this paper.

BELLOTTIA GIGLIOLI, 1883

Bellottia Giglioli, 1883, p. 399, type species *Bellottia apoda* Giglioli by monotypy.

Diagnosis: Chin barbels absent. Gill membranes separate from each other and from the isthmus. Livebearing; copulatory apparatus (Turner, 1946) of male consisting of a urogenital sinus enclosing a penis which protrudes from the urinogenital sinus and a smaller papilla at the base of the sinus; no claspers or ossified intromittent organ. Ventral fins absent. Vertical fins confluent, covered with thin skin through which the rays are easily visible. Pectoral fin entire, without separated elongate rays; supported on a broad fleshy pad, but not on an elongated peduncle. Caudal fin rays 6. Head with a patch of scales behind the eye and jaw, otherwise naked, bearing prominent papillae and large pores.

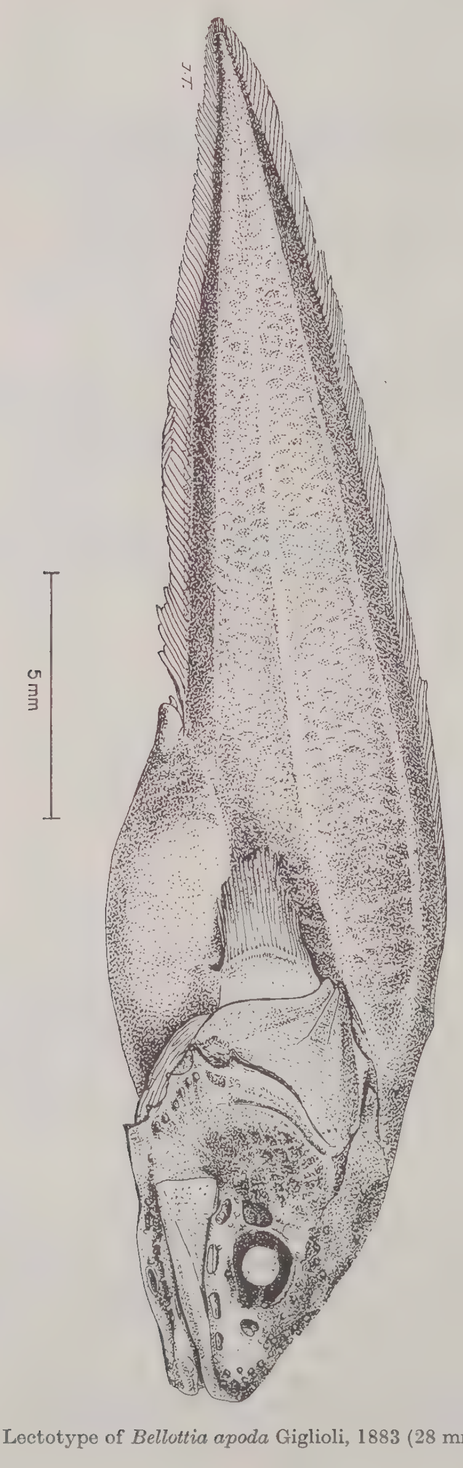

Fig. 1. Lectotype of *Bellottia apoda* Giglioli, 1883 (28 mm Std. l.).

Anterior nostril a thin-walled tube located above the upper lip. Developed gill rakers 3 or 4. Spine on opercle flattened. Branchiostegal rays 7(?). Body relatively short; snout depressed but not markedly so. Lateral line in two sections, an upper and a lower, marked by lines of papillae. Teeth present on premaxillary, vomer, palatine and dentary; maxillary vertically expanded posteriorly. Eyes developed, at surface of head. Body completely covered with small, imbricate scales. Peritoneum pale.

First neural spine short, middle precaudal neural spines depressed; not truncate at their tips; ribs lacking on first two centra; ribs on centrum three directed anteriorly in the male, ventrally in the female; ribs on vertebrae 3 to 7 inserted on centra; ribs on vertebrae 8 to 10 at ends of parapophyses; centra 11 and 12 with parapophyses but no ribs. Vertebrae $12+35=47$. Some ribs with epipleurals.

Relationships

Among the numerous genera of viviparous ophidioids, *Bellottia* bears at least superficial resemblance to about half a dozen genera of small, mostly dark-colored fishes that are probably all restricted to relatively shallow waters and have a copulatory apparatus with no ossified parts or hard, paired claspers. *Bellottia* may be distinguished immediately from all of them by its lack of ventral fins. Unlike the three related genera (*Oligopus* Risso, 1810; *Stygnobrotula* Böhlke, 1957; and *Grammonoides* Smith, 1947) *Bellottia* has palatine teeth. Also, *Oligopus* has truncate precaudal neural spines, while these spines are pointed in *Bellottia*. *Brosmophyciops* Schultz, 1960; and *Bidenichthys* Barnard, 1934; (and the larger, medium depth genus *Brosmophycis* Gill, 1862) have free caudal fins and ribs on the first two vertebrae, and in addition *Bidenichthys* has an elongate peduncle supporting the pectoral fin; *Bellottia* has confluent vertical fins, no ribs on the first two vertebrae and a normal pectoral fin support. *Calamopteryx* Böhlke & Cohen, 1966 has ribs on the first centrum, has an elongate pectoral fin peduncle and has some ribs, expanded distally (? for swimbladder support); *Bellottia* has no expanded ribs.

The viviparous ophidioid genera are not well known, and they differ in such a variety of ways that although we can easily point out many differences, an attempt to distinguish phylogenetically significant similarities is difficult. Bearing this difficulty in mind, we suggest that the closest known relative of *Bellottia* may be *Microbrotula* Gosline, 1953; which differs most obviously in having ventral fins, ribs on the second centrum and some ribs expanded. Some characters in which both agree, and in which they differ from various of the genera discussed above are: a short first neural spine; precaudal neural spines with pointed tips; confluent vertical fins; palatine teeth present; posterior end of maxillary expanded; few caudal fin rays (four in *Microbrotula*); prominent papillae and pores on head; small eyes, and a large nasal organ.

Specimens examined in preparing the foregoing section are listed in Cohen (1964) and Böhlke & Cohen (1966). In addition, the types of *Brosmophyciops pautzkei* Schultz, 1960, in the U.S. National Museum were examined, as was a specimen of *Bidenichthys capensis* Barnard, 1934. Specimens of *Brosmophycis marginatus* Ayres, 1854, from the Scripps Institution of Oceanography were examined. X-ray photographs and in some instances alizarin preparations were used.

Résumé of opinions

Giglioli (1883, pp. 399–400) stated that *B. apoda* is undoubtedly related to *Pteridium atrum* (Risso, 1810) (=*Oligopus ater* Risso, 1810). He pointed out that many characters, both meristic and morphometric, agree, while the two species differ from each other in the lack of ventral fins in *B. apoda*, in the dentition, condition of the gill-rakers and in the form of the lateral line. He referred *Bellottia* to a special division of the group Brotulina, characterized by the lack of ventral fins. Giglioli gave the following meristic characters: D 90, A 75, C 12, branchiostegal rays 4.

Emery (1886, pp. 157–8) studied the Naples specimen, which was larger than the two type-specimens in Florence. He published four illustrations (pl. 10) of the specimen, mainly in order to show the lateral line system and the 'canali mucosi' on the head. He considered *Bellottia* a transitional form between the Brotulini (in which he placed one species, *Pteridium atrum*) and the Fierasferini. *Bellottia* resembles the former in its possession of a caudal fin while the lack of ventral fins makes it like the Fierasferini. He gave the following meristics based upon the specimen from the Stazione Zoologica: D 85, A 66, C 10, P 23, V 0, branchiostegal rays 5.

Vaillant (1888, pp. 282–5) compared *Bellottia* to *Alexeterion* Vaillant, 1888. In spite of many differences he considered it possible that the two genera formed a transitional group between the Fierasferina and the Brotulina, but showed most resemblance to the latter.

Goode & Bean (1896, pp. 343–4) gave an abbreviated translation of the original description and stated that 'the genus is admitted to this work not only for the purpose of comparison, but in the belief that it will eventually be found in deep water'.

Zugmayer (1911*b*, p. 131) found that *Leucochlamys* (Zugmayer, 1911 *a*) differed from *Bellottia* in lacking scales, lateral line and palatine teeth.

D'Ancona (1939, pp. 166–7) also suggested relationship between *Bellottia* and *Pteridium*, the most important disagreement between the two being the absence of ventral fins in *Bellottia*. He mentioned and illustrated the larval specimen from the Strait of Messina.

Norman (1939, p. 80, and 1966, p. 499) remarked that *Bellottia apoda* is probably based upon larval or post-larval forms, believed to belong to the Brotulidae.

Padoa (1956, pp. 754–5) found it remarkable that the larva from the Strait of Messina is 35 mm long while the adult type material from the Gulf of Naples is less than 30 mm long. Padoa's treatise is based upon earlier Italian papers on this species.

Tortonese (1963, p. 179) questioned the genus and species.

Material examined (two specimens):

Lectotype (♂, 28 mm Std. l.); Gulf of Naples; depth 30 m; *Posidonia*-bottom; trawl. 20–12–1882. Zool. Mus., Florence. (Cat. No. 2176.)

Paralectotype (♀, 25·5 mm Std. l.); idem. Zool. Mus., Florence. (Cat. No. 2176.)

Seven specimens have been referred to *B. apoda*. Originally, five specimens were caught in the same haul in the Gulf of Naples. According to Giglioli (1883), the two specimens here examined were the only ones on which the description was based. Giglioli did not select a holotype and no illustration was published with his description. Both the type-specimens were placed in Florence. We here select the larger of the syntypes (a male) as lectotype. Two of the remaining three specimens were deposited in the Museo Civico, Milan, and one in the Stazione Zoologica, Naples. Correspondence with colleagues at these two institutions revealed that the Milan specimens were lost during World War II and that the specimen in Naples has also disappeared. According to Giglioli, one of the three missing specimens measured about 50 mm, but Padoa (1956, p. 754) gave 42 mm as the maximum length. None of the earlier authors stated whether their measurements were of standard length or total length. D'Ancona (1939, p. 166) mentioned two additional specimens from the Zoological Museum, Florence. One was caught in the Gulf of Naples, 29–3–1888, and the other in the Strait of Messina, 10–4–1895. The former was designated 'esemplare' and the latter 'larva'. Nielsen (1966) showed that these two specimens do not belong to *B. apoda*, but are both larval specimens of another brotulid genus, *Oculospinus* Koefoed, 1927. Besides the five specimens discussed above, some additional specimens may have been caught, as Giglioli (1883, p. 400) mentioned that a taxidermist from Naples had written him that he had kept *Bellottia* alive in aquaria. The identification of these latter specimens has not been confirmed, and they may have been *Oligopus ater*.

Description

Meristic and morphometric characters are given in Tables 1 and 2.

Table 1. *Meristic and morphometric characters in* Bellottia apoda

	Lectotype (♂)	Paralectotype (♀)
Standard length	28	25·5
Meristic characters		
Dorsal rays	93	89
Caudal rays	6	6
Anal rays	77	69
Ventral rays	0	0
Pectoral rays (d-s)	23–23	22–
Branchiostegal rays	7?	7?
Gill rakers on anterior arch	2/4+7	2/3–4+9
Vertebrae (incl. urostyle)	12+35	12+35
Scales in lateral line	65–70	65–70
First anal ray below D-ray no.	17	18
First anal ray below vertebra no.	15	15
First dorsal ray above vertebra no.	8	8
Morphometric characters in mm and in % of standard length		
Head	7·9 (28·0)	7·8 (30·5)
Depth at ant. D	6·3 (22·5)	—
Snout	2·0 (7·2)	2·1 (8·2)
Upper jaw	4·2 (15·0)	4·0 (15·5)
Diameter of pigmented eye	1·5 (5·4)	1·3 (5·1)
Probable bony interorbital	1·9 (6·8)	1·7 (6·7)
Total interorbital	2·7 (9·7)	2·8 (11·0)
Preanal	13·8 (49·5)	13·0 (51·0)
Predorsal	11·0 (39·5)	10·2 (40·0)

Table 2. *Number of gill rakers in* Bellottia apoda

Arch	♂	♀
1	2/4+7	2/3–4+9
2	0/11	1/13
3	0/9	0/11
4	0/8	0/8
5	0	0

The head is somewhat depressed. There is a flattened spine at the dorsal part of the operculum and four smaller spines on the preopercular margin, of which the two middle ones are the largest. The posterior end of the maxillary is vertically expanded and situated posterior to the eye. The posterior nostril is close to the eye and the smaller, anterior nostril (not shown in the illustration) is near the tip of the snout close to the jaw. The otoliths are large. A swimbladder is present and the long intestine is somewhat coiled.

Fins. Vertical fins united. The dorsal fin originates above the pectoral fin base, and the anal originates approximately midway between the snout and the caudal fin. The pectoral fin is inserted medially on the body. Ventral fins absent.

Scales. The scales are cycloid, imbricate and approximately 0·2 mm in diameter. Although few scales remain on the male, it is possible to estimate the number of lateral line rows from the scale-pockets; more scales remain on the female. A patch of barely imbricate scales is present on the preoperculum and posterior to the maxillary.

Lateral line. The female has a double row of lateral line papillae anteriorly on the body. The lower row follows the midline almost to the caudal fin, but the upper row, in which there are longer interspaces between the papillae, ends slightly posterior to the level of the anus. The lateral line is difficult to distinguish in the male. Papillae are distributed on the head, but only the prominent ones are shown on the figure.

Dentition. Premaxillaries with small, pointed, close-set teeth arranged in approximately five rows anteriorly, gradually decreasing to a single row posteriorly. The arch-shaped vomerine dentition consists of one to two rows of teeth similar in size to those in the premaxillaries. The dentaries have many, small, pointed teeth, of which a few are enlarged.

Gill arches. Only the anterior arch is provided with elongated rakers, varying in number from three to four. Both these and the poorly developed rakers are dentigerous. Figure 2 shows the anterior, left gill arch of the lectotype. The gill laminae are shorter on the anterior than on the following arches; there are 9 on the upper and 28 on the lower arm of the anterior arch of the lectotype, all with a featherlike composition. Except for the anterior arch the rakers in the outer and the inner row are equally developed. Table 2 gives a survey of the number of rakers from both sides of the two specimens.

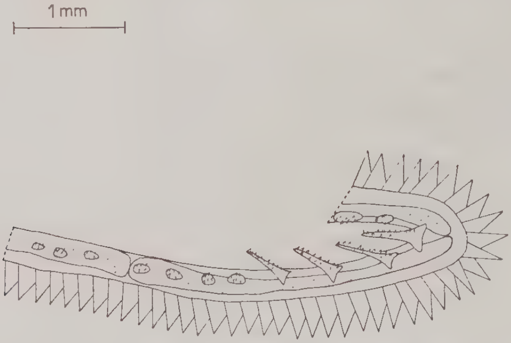

Fig. 2. Anterior left gill arch of the lectotype of *Bellottia apoda* Giglioli, 1883.

Vertebrae and ribs. 12 precaudal and 35 caudal vertebrae. All the vertebral centra are hour-glass shaped. The neural and haemal spines are all pointed and all of the former have large bases. The first neural spine is shorter than the second and the middle precaudal neural spines are somewhat depressed. The first and second centra lack ribs, the 3rd–7th centra have ribs attached (those on the 3rd centrum are turned anteriorly in the male and ventrally in the female). Ribs on the 8th–10th vertebrae insert at the ends of parapophyses. No ribs on the 11th–12th vertebrae. Parapophyses developed only on the 8th–12th vertebrae.

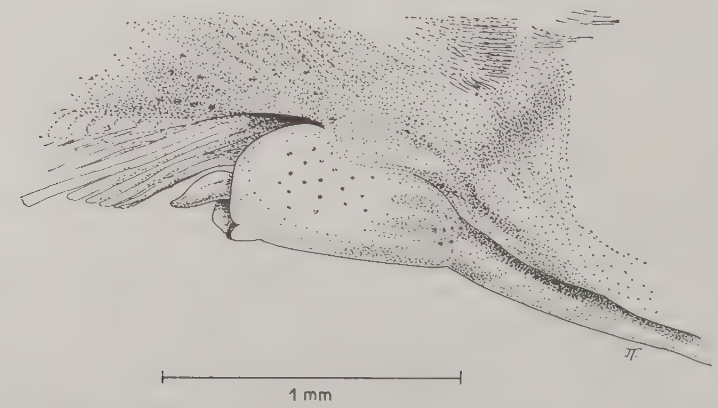

Fig. 3. Copulatory apparatus of the lectotype of *Bellottia apoda* Giglioli, 1883 (♂).

Gonads. Parts of the gonads of both specimens were cleared and stained. Sections showed that the lectotype is a male and the other a female. This corresponds with the presence in the lectotype of a prominent urinogenital sinus covering a long penis (Fig. 3). The second specimen has a poorly developed urinogenital sinus and lacks a genital papilla. The penis is not ossified and is midway between the base and the tip of the urinogenital sinus. A smaller papilla is present at the base of the sinus. Nielsen, Munk & Jespersen (MS) have demonstrated the presence of spermatophores in some ophidioid species, i. a. in *Bellottia apoda*. One 3-mm long testis contains numerous bundles of long-tailed spermatozoa, and all the bundles in the dorsal duct of the testis have firm capsules. The ovaries (2·5 mm long) contain few eggs, in a very early stage of development. Most of the ovarian lumen is filled with spermatophores with intact capsules. The sections showed no traces of hermaphroditism.

Biology. The presence of spermatophores in the female proves that this dioecious species has internal fertilization. The presence of few and small eggs suggests that the female is able to store the spermatophores until the eggs are ripe.

Both the specimens were caught in the same haul of a bottom trawl at a depth of 30 m in the Gulf of Naples. We suggest that few specimens have been caught because *Bellottia* lives in holes and crevices of rocks and corals like related genera. This type of habitat has been poorly sampled for fishes in the Mediterranean. The only determinable stomach contents were a 7 to 8 mm long mysid, in the male.

Distribution. Known only from the type locality in the Gulf of Naples.

ACKNOWLEDGEMENTS

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CURRENT AMERICAN LITERATURE IN THE MARINE SCIENCES

by

H.S. Nishimura
Bureau of Commercial Fisheries Biological Laboratory
Honolulu, Hawaii

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H.S. Nishimura
Bureau of Commercial Fisheries Biological Laboratory
Honolulu, Hawaii

ABSTRACT

The current American literature of the marine sciences is widely scattered. This paper presents selected lists of presently available books and monographs; serial publications, including scientific journals, newsletters, and trade journals; specialized indexes; atlases; series of technical reports; and collections of contributions.

INTRODUCTION

Literature in the marine sciences has been increasing with prodigious speed in recent years. In 1958 the library of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, included 2,030 books and monographs and 324 serial publications. By 1965, although acquisitions were carefully restricted to publications that bear directly on oceanography and marine biology, the library had grown to 3,106 books and monographs and 404 serial publications--a growth of about one-third in 7 years.

In connection with the Symposium on Fisheries Education and Training of the 12th Session of the Indo-Pacific Fisheries Council (IPFC), Honolulu, Hawaii, October 3-17, 1966, I was asked to assemble a display of books in the marine sciences that are currently available from American publishers. Other agencies were asked to provide displays of British and Japanese books. It occurred to me that, useful though such a list of books might be, much of the pertinent literature in the marine sciences would be ignored if other media of publication were not mentioned. I have therefore listed here not only books and monographs, but also serial publications (including newsletters and trade journals), indexes, atlases, technical reports, and series of contributions which carry material pertaining to the marine sciences.

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*IPFC/C66/SYM 33.

Needless to say, such lists must have many oversights. My only excuse is that the field is large and complex and one particularly subject to value judgments. I have tried to choose those documents in print, and hence readily available, which might be of most use to someone who is beginning to build a special library in the marine sciences.

For more comprehensive lists, and particularly for references to many of the very important publications that are now out of print and which I have not cited, one may consult:

Aquatic Biology and Oceanography; A Selected List of Books, by Paul T. Macy and Ida K. Johnson. U.S. Fish and Wildlife Service, Fishery Leaflet 541, January 1963, 9 pp.

Bibliography of Marine Sciences Publications and Reports (1962-1964), issued by the Interagency Committee on Oceanography of the Federal Council for Science and Technology, ICO Pamphlet 20. (In preparation.)

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Books and Aquatic Biology: Fresh-water and Marine, prepared for the Biological Sciences Communications Project, by Carl R. Keeler. Biological Sciences Communication Project, George Washington University, Washington, D.C., June 1963, 45 pp.

A Reader's Guide to Oceanography, prepared by Jan Hahn, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, rev. ed., November 1964, 13 pp.

BOOKS AND MONOGRAPHS

The following books and monographs were assembled for the IPFC display. Several members of the scientific staff of the Laboratory in Honolulu advised me in preparing the list, which is in the nature of a "basic" list of currently available books for the small library. A few Canadian books are included, since they are readily available in the United States.

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American Fisheries Society, Washington Building, 15th and New York Avenue, N.W., Suite 1040, Washington, D.C. 20005

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TECHNICAL REPORTS

Before World War II, technical reports were relatively few. However, the requirements of Government contracts for rapid publication (and the inexpensiveness of the processes used for publication) have led to a proliferation of these reports in recent years. The Federal Government alone now maintains four important agencies which reproduce and distribute technical reports prepared on Government-supported research. In 1964 more than 1 million such reports were made available by these agencies, and the number is growing rapidly. Technical reports present difficulties in handling to librarians, for often such conventional bibliographical aids as the main catalog entry, year and place of publication, pagination, etc. are omitted. Nevertheless, in special libraries such as those devoted to marine sciences, technical reports are becoming recognized as legitimate means of communication and are accessioned, catalogued, and processed in much the same manner as books and monographs.

An exhaustive, thoroughly indexed list of technical reports dealing with the marine sciences apparently does not exist. Some lists have been made by a few of the marine laboratories, which issue a bibliography of reports and accessions lists on a regular basis. Librarians must rely upon these, upon lists published by Government agencies, and upon personal communications among scientists to remain current with the technical report literature.

Some of the American technical report series particularly relevant to fishery biology and oceanography are:

Data Reports, Department of Oceanography, Oregon State University, Corvallis, Oregon.

Data Reports, Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92038

Data Reports, U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries, Washington, D.C. 20402

IGY Oceanography Report Series, World Data Center A: Oceanography, Washington, D.C. 20390

Reports (Mimeographed), Institute of Marine Science, University of Miami, Miami, Florida 33149

Scientific Reports, Institute of Geophysics, University of Hawaii, Honolulu, Hawaii

Special Scientific Reports, Marine Laboratory, Florida State Board of Conservation, St. Petersburg, Florida

Technical Reports, Chesapeake Bay Institute, Johns Hopkins University, Baltimore, Maryland 21218

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Technical Reports, Department of Oceanography, University of Washington, Seattle, Washington 98105

Technical Reports, Lamont Geological Observatory, Columbia University, Palisades, New York 10964

Technical Reports, Narragansett Marine Laboratory, University of Rhode Island, Kingston, Rhode Island 02881

Technical Reports, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

COLLECTIONS OF CONTRIBUTIONS

Significant contributions to the marine sciences often appear in journals that at first glance may seem very unlikely repositories for such information. For this reason, particularly useful to the special librarian, especially one whose means are small, are the collections of Contributions issued annually by several institutions and usually available to libraries upon exchange.

These include reprints of papers published by staff members during a certain period, usually a year. As a rule, they are available upon request. Some institutions use them only as library exchanges.

Among the Contributions most valuable to the librarian in the marine sciences are those of:

Department of Oceanography, Oregon State University, Corvallis, Oregon

Department of Oceanography and Meteorology, Texas A & M University, Galveston, Texas

Hawaii Marine Laboratory, University of Hawaii, Honolulu, Hawaii

Narragansett Marine Laboratory, University of Rhode Island, Kingston, Rhode Island

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ACKNOWLEDGEMENTS

The impetus for this paper came from the request of G.L. Kesteven, Convener of the Symposium on Fisheries Education and Training, to assemble a collection of American books in the marine sciences for display at the 12th Session of the Indo-Pacific Fisheries Council. The help of several members of the scientific staff of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, was appreciated. American publishers supplied mint copies of requested volumes for display at the 12th Session.

Tagging of Skipjack Tuna (*Katsuwonus pelamis*) in Palau

by

Tamio OTSU
Bureau of Commercial Fisheries Biological Laboratory
Honolulu

The Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, initiated a skipjack tuna tagging program in the Palau Islands, Western Carolines, in June 1967 in cooperation with the Government of the Trust Territory of the Pacific Islands. As of mid-March 1968 five tagged fish have been recovered.

Reprinted from Report of the Symposium on the Cooperative Study of the Kuroshio and Adjacent Regions (CSK), Report and Abstracts of Papers, FAO Fisheries Report No. 63, p. 42, 1968.

Made in United States of America
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pp. 399–401

ABNORMAL FRESHWATER FISHES IN WASHINGTON STREAMS.—Abnormal fish continue to be interesting biological curiosities and have been reported for many species throughout the world (Dawson, 1964, 1966). Of 100,000 freshwater fish captured in 1957–65 in the State of Washington by personnel of the Bureau of Commercial Fisheries, 236 abnormal individuals were discovered. These are listed by species and type of abnormality (Table 1). Factors that may have influenced the occurrence of abnormal fish in one unusually productive stream are briefly discussed.

Streams from which the deformed fish were collected are listed in Table 1. The Yakima River and Shea Creek are in the eastern drainage of the Cascade Mountains; other streams are in the coastal or western drainage. Shea Creek, unnamed on existing maps, is south of Ellensburg. It derives water from nearby springs, an irrigation diversion of the Yakima River, and from field drainage.

The fish were collected mostly by electrofishing, but some were trapped by a weir in Shea Creek. They were not critically examined for abnormalities; only gross external differences were noted. Some fish were examined radiographically. Lengths were measured in mm from tip of snout to fork of tail. The abnormalities were suspected to have occurred at an early developmental stage. Not considered, therefore, were aberrations incurred later. One example would be atrophy of the pectoral fin (found on young fish in the lower Yakima River) caused by the copepod parasite, *Lernaea* sp.

Types of abnormality, by stream, are also listed in Table 1. Vertebral defects occurred in more species than any other anomaly, followed by pelvic and caudal fin aberrations. The greatest number of deformities in individual fish, however, were of the pelvic fin and girdle. Vertebral abnormalities were visible externally from lateral and vertical body humps or stubby appearance; radiographs showed that these deformities originated from curvatures of the spinal column and from fused or compressed vertebrae. This abnormality often greatly impaired swimming.

Eight fish with curvature of the spinal column had additional major deformities. Four speckled dace (*Rhinichthys osculus*) with vertebral curvature in the peduncle region also had unexpanded caudal fins; two lacked pelvic fins; and one, lacked pelvic fins and had a reduced number of anal fin rays. One redside shiner (*Richardsonius balteatus*) had a spinal column sharply decurved at the ante-penultimate vertebra; hypural and caudal development was also abnormal. Abnormal caudal fins of the speckled dace, redside shiner, and chiselmouth (*Acrocheilus alutaceus*) occurred in conjunction with vertebral deformities in the caudal peduncle.

Pelvic fin abnormalities included fusion and various degrees of degeneration in one or both fins or absence of both. A largescale sucker (*Catostomus macrocheilus*) had additional hypural plates and rays in the dorsal lobe; a bridgelip sucker (*Catostomus columbianus*) had expanded hypural plates and a double, unexpanded, caudal fin. Four speckled dace had anal fins with two to four rays, where seven is normal. A prickly sculpin (*Cottus asper*) had its posterior dorsal portion of the body greatly reduced; the dorsal fin consisted of 13 rays where 19 is normal.

In abnormalities of the head, one brook trout (*Salvelinus fontinalis*) had a jaw projecting beyond the snout; a largescale sucker had a mouth rotated to the right; and a shorthead sculpin (*Cottus confusus*) had a "pughead."

Abnormal fish appeared to be more prevalent and their malformations more severe in Shea Creek than in the other streams. Because studies had indicated little movement of fish to and from Shea Creek, I assume that most of the deformed fish originated there. For four years, many abnormal fish of different species were consistently collected from various brood years. Nine general types of abnormality were discovered in seven species (Table 1). The greatest number of abnormal fish from Shea Creek were speckled dace—correlated with their abundance. In a group of abnormal speckled dace collected in April 1963, pelvic fins were absent or degenerate in 0.46%, and spinal curvature was present in 0.12% (Table 2). The limited data in Table 2 does not suggest an increasingly greater mortality

TABLE 1. NUMBER OF FISH WITH DIFFERENT TYPES OF ABNORMALITIES THAT WERE COLLECTED FROM 1957 TO 1965. Fork length (mm) in parentheses.

			Type of Abnormality								
Stream	Species	No. of Fish[1]	Vertebral	Pelvic Fused	One Pelvic Absent	Both Pelvics Absent	Degenerate Pelvic	Caudal	Anal	Head	Body
Shea Cr.	Salmonidae										
	Oncorhynchus tshawytscha	1	1(67)								
	Salvelinus fontinalis	6	5(54–181)							1(83)	
	Cyprinidae										
	Acrocheilus alutaceus	2	1(144)			1(68)					
	Rhinichthys osculus	181	33(35–75)		20(43–83)	130(34–79)	11(34–79)	4(42–60)	4(40–60)		
	Richardsonius balteatus	20	9(43–90)		2(69–111)	9(38–83)		1(90)			
	Catostomidae										
	Catostomus columbianus	7	1(144)	1(84)	1(137)	3(66–115)		1(116)			
	C. macrocheilus	4	1(228)			1(80)	1(80)	1(335)		1(120)	
Yakima R.	Cyprinidae										
	Acrocheilus alutaceus	3	2(53–59)			1(81)		1(59)			
	Ptychoceilus oregonensis	1	1(35)								
	Rhinichthys cataractae	1				1(58)					
	Centrachidae										
	Micropterus dolomieui	1	1(61)								
Newaukum Cr.	Salmonidae										
	Oncorhynchus kisutch	1	1(82)								
Rock Cr.	Cottidae										
	Cottus confusus	1								1(74)	
	Salmonidae										
	Salmo gairdnerii	1	1(29)								
Rocky Cr.	Salmonidae										
	Salmo gairdnerii	1			1(173)						
Elokomin R.	Cottidae										
	Cottus aleuticus	1	1(54)								
Abernathy Cr.	*C. asper*	1									1(92)
Soos Cr.	*C. rhotheus*	3	3(68–99)								
Total abnormalities			61	1	24	146	12	8	4	3	1

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[1] Some fish had more than one type of abnormality.

Table 2. Normal and Abnormal *Rhinichthys osculus* by Body Length from Shea Creek in April 1963

Fork Length (mm)	Total No. of Fish	% Composition		
		Normal	Missing Pelvic	Vertebral Curvature
41– 49	2130	99.45	1.22	0.33
50– 59	5529	99.58	0.31	0.11
60– 69	3483	99.89	0.11	—
70– 79	1140	99.03	0.79	0.18
80– 89	290	99.31	0.69	
90– 99	60	100.00		
100–109	9	100.00		
110–119	1	100.00		

with age (as indicated by length) for the abnormal than for the normal speckled dace.

The only severely deformed fish from waters other than Shea Creek were the rainbow trout fry from Rock Creek and the torrent sculpin from Soos Creek (both with vertebral curvature). In a study of Boise Creek, King County (Miller, 1965), 1715 speckled dace, including a few longnose dace (*Rhinichthys cataractae*), were examined for abnormalities—none were found. With a probability of 0.0058 (that observed for Shea Creek dace with missing pelvics or vertebral curvature), four abnormal fish with vertebral curvature or missing pelvics should have appeared in the Boise Creek sample.

Factors causing a high percentage of abnormal fish or enabling them to survive in Shea Creek are unknown, but subject to speculation. Shea Creek is small and stable, has a silt bottom with occasional rocky riffles, and is highly productive. Profuse growths of water weeds, *Anacharis* sp. and *Potamogeton* sp., restrict water flow and harbor large populations of the amphipod, *Hyallela azteca*, and aquatic insects. The fish fauna, consisting of 14 species, is extremely abundant.

The exact mechanics of natural selection are difficult to study and should be more severe under poor survival conditions. This factor may apply to Shea Creek. The presence of many severely deformed fish (some of a mature size) shows that some factor or factors permitted their survival.

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Benjamin G. Patten, *Bureau of Commercial Fisheries Biological Laboratory, 2725 Montlake Boulevard East, Seattle, Washington 98102.*

The Porpoise and the Tuna

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The Porpoise and the Tuna

By William F. Perrin
U.S. Bureau of Commercial Fisheries
Fishery-Oceanography Center
La Jolla, California

"Porpoise!"

The lookout spots a large school near the horizon. The tuna boat slows and stops, and two fast, outboard skiffs, or pongas, are lowered into the water. The drivers, in life jackets and crash helmets, strap themselves into their seats and check their radio headsets. They give a signal, and the boat gets under way, the pongas following close astern. The school is much closer now, and the skipper scans it with powerful binoculars, searching for signs of tuna. He sees jumping fish, and the real action begins.

The mastman in the crow's nest signals the chasers and they surge forward across the tops of the swells. He directs them by radio as they flank and harry the porpoise school, trying to tighten it and slow it down. The mastman calls, "Stand by!" and the deck crew gets ready to release the net.

The chasers are running ahead of the school now, and the porpoise are beginning to mill in a tight circle. The mastman shouts, "Let her go, let her go!" and a big skiff drops into the water from its perch atop the net pile on the fantail, pulling the end of the net with it. The boat circles the porpoise school at full speed, and the huge stack of webbing on the net platform melts swiftly as the half-mile long seine pays out.

The mastman gives directions to the helmsman on the bridge and at the same time coordinates the movements of the two chaser pongas, trying to keep the school together until the set is completed. Success. The entire school, a thousand porpoise or more, has been encircled. As the boat completes the circle, the other end of the net is picked up from the big skiff, and pursing begins. The purseline, acting as a huge drawstring, gathers up the bottom of the seine and in a few minutes the net is closed. Now begins the long, hard job of hauling and emptying the net.

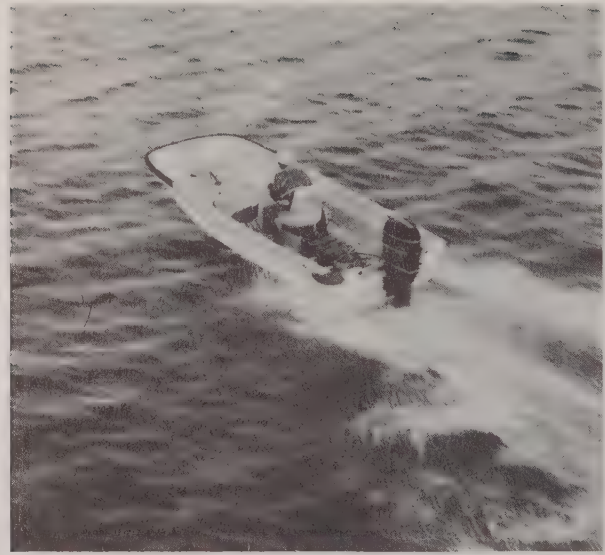
Why Herd Porpoise?

What sort of fishing is this? Why are porpoise herded and captured when the object is to catch tuna? Tuna fishermen have known for a long time that porpoise and tuna are often found together. Since porpoise are larger and usually make more commotion at the surface than tuna, they can be seen at greater distances, and the fishermen

LOOKING FOR PORPOISE *to find tuna, a lookout searches the horizon. Porpoise and tuna are often found together. Since porpoise are larger and usually make more commotion at the surface, they can be seen at greater distances. (William F. Perrin)*

spot tuna by looking for porpoise. Until the advent of durable, lightweight nylon webbing and hydraulic net-hauling gear in the late 1950's, almost all of the U.S. tuna catch was taken with hook-and-line. By 1960, most of the tuna baitboats had been converted to purse-seiners.

The purse-seiners used the same spotting techniques as the baitboats, locating tuna by locating porpoise. The seiners soon discovered that the porpoise-tuna association is much closer than had been suspected. Unless a large portion of the porpoise school is encircled along with the tuna, the set is usually unsuccessful—a "skunk." Sometimes even a few escaping porpoise can lead all the fish with them out of the net. When the fishermen found that the porpoise can be herded, they began to use fast, outboard pongas for this purpose, and "porpoise fishing" rapidly evolved in techniques and efficiency. Catch and landing records compiled by scientists of the



LEFT: A CHASER PONGA, *directed by radio, roars off to intercept a porpoise school. (William F. Perrin)*

RIGHT: THE COMMON DOLPHIN, *or white-belly porpoise, (top) is sometimes found in association with tuna in the waters off Baja California and in the Gulf of California. Spinners (bottom) are shown swimming at the bow of a boat. (Roger E. Green)*

Inter-American Tropical Tuna Commission show that in 1966 about 62 per cent of the seine-caught yellowfin tuna from the eastern tropical Pacific was captured from schools associated with porpoise.

Improved Methods More Humane

Initially, the fishermen did not know how to get rid of the porpoise once they had them in the net, so they hauled the entire contents of the net on board, sorted out the fish, and threw the porpoise overboard, often injuring or killing many of them. This procedure involved a great deal of extra work and time. Through considerable experimentation, the fishermen developed a more efficient and more humane method.

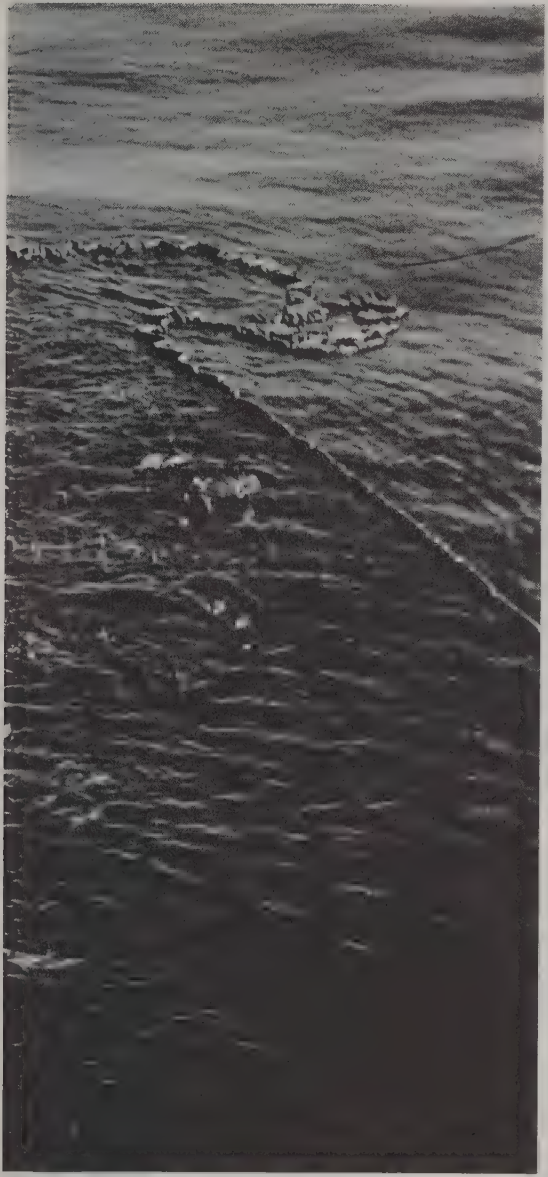
In the last few years, most of the boats in the fleet have adopted a method called "backing down." Approximately one-half of the net is taken aboard and secured, and a large bag, or balloon, is produced in the net, near the boat. A crewman in the crow's nest watches the tuna as they run back and forth in the net. He also watches the porpoise, which usually stay in a very tight group away from the boat in the far end of the net. When the fish are in the balloon area, the lookout signals the bridge and the boat backs down, sinking the corkline at the far end of the net and spilling most of the porpoise. Great care must be taken to avoid losing the tuna. The operation allows nearly all the porpoise to escape, but a few are usually drowned or badly injured because they become entangled in the webbing or refuse to cross the corkline. The fishermen try to rescue these animals, often at considerable risk to themselves.

Three Species of Porpoise

At least three species of porpoise are found together with tuna in the tropical fishery: a spotted form, *Stenella graffmani;* the more slender, long-snouted *Stenella longirostris;* and a third as yet unidentified species. The first two are called spotters and spinners, respectively by tuna fishermen. The spinners are so named because of

their spectacular habit of leaping high out of the water and rotating several times in mid-air. The reason for this behavior is unknown, although courtship display and just plain exuberance have been suggested. The trainers at Sea World Park in San Diego, California, have succeeded in teaching a bottlenose porpoise, *Tursiops truncatus,* to perform a similar rotating lèap, but thus far only the spinners are known to behave this way in the wild.

Schools of animals of the third species—a porpoise with white markings, which may be the common dolphin or saddleback, *Delphinus delphis*—have been seen together with tuna off Costa Rica. The fishermen have been unable to herd or catch these porpoise or the fish with them and call them "the un-



SEVERAL HUNDRED SPOTTER PORPOISE *make up this large school. The seine has just been pursed and hauling has begun. (William F. Perrin)*

touchables." The common dolphin does occasionally occur together with tuna farther north along the coast of Baja California and in the Gulf of California where it is called whitebelly by the fishermen, but most of the fishing in this area is not carried out in this manner.

Spotted and spinning porpoise may occur alone or in mixed schools. A school may consist of a few individuals or a thousand or more. The associated fish—which may amount to less than 100 fish or to more than 100 tons—are yellowfin tuna, *Thunnus albacares,* or (less often) skipjack tuna, *Katsuwonus pelamis,* or both. Oceanic birds, such as frigate birds, boobies, and others, may also make up part of the association.

Why Porpoise and Tuna Together?

Why do the tuna and porpoise occur together? Although the fishermen benefit by the association of tuna with porpoise schools, the basis of the association is unknown. Some possible explanations that may be considered are that the relationship is allied to feeding, or that the tuna gain protection against sharks, or else tuna are attracted to any object, living or nonliving, which can be of aid in spatial orientation.

One possible explanation of the association is that the porpoise and tuna feed on the same things and thus are found together in areas of high food concentration. Biologists of the Inter-American Tropical Tuna Commission at La Jolla, California, looked at thousands of yellowfin tuna stomachs and found them to contain representatives of forty-four fish families and twelve invertebrate orders, including crustaceans, molluscs, tunicates, and cephalopods (squid and octopi). Even such items as kelp, bits of wood, and feathers were found. Stomach contents of skipjack tuna were similarly diverse. Most of the food of both species, however, was made up of fish, squid, and decapod crustaceans. Not much is known about the diets of porpoise associated with tuna.

A Bureau of Commercial Fisheries biologist recently examined the stomach contents of tuna and porpoise caught in the same hauls and found some overlap of food items. The porpoise and tuna stomachs contained squid and small fish, but the tuna also contained large numbers of pelagic crabs, which were absent in the porpoise. These findings seem reasonable, since it is a general rule of animal community organization, at least in terrestrial and littoral communities, that forms which occur in close proximity to each other do not usually make use of the same resources at the same time or in the same manner. Thus, one might not expect the closely associated tuna and porpoise to compete for food. They may feed at different times of the day, possibly on different local concentrations of food. It must be noted, however, that the science of pelagic ecology is in its infancy, and the general rules which apply to terrestrial and littoral communities may not be valid on the high seas. Much more investigation of the distribution of food and the feeding habits of tuna and porpoise is needed before the common-food hypothesis can be accepted or rejected.

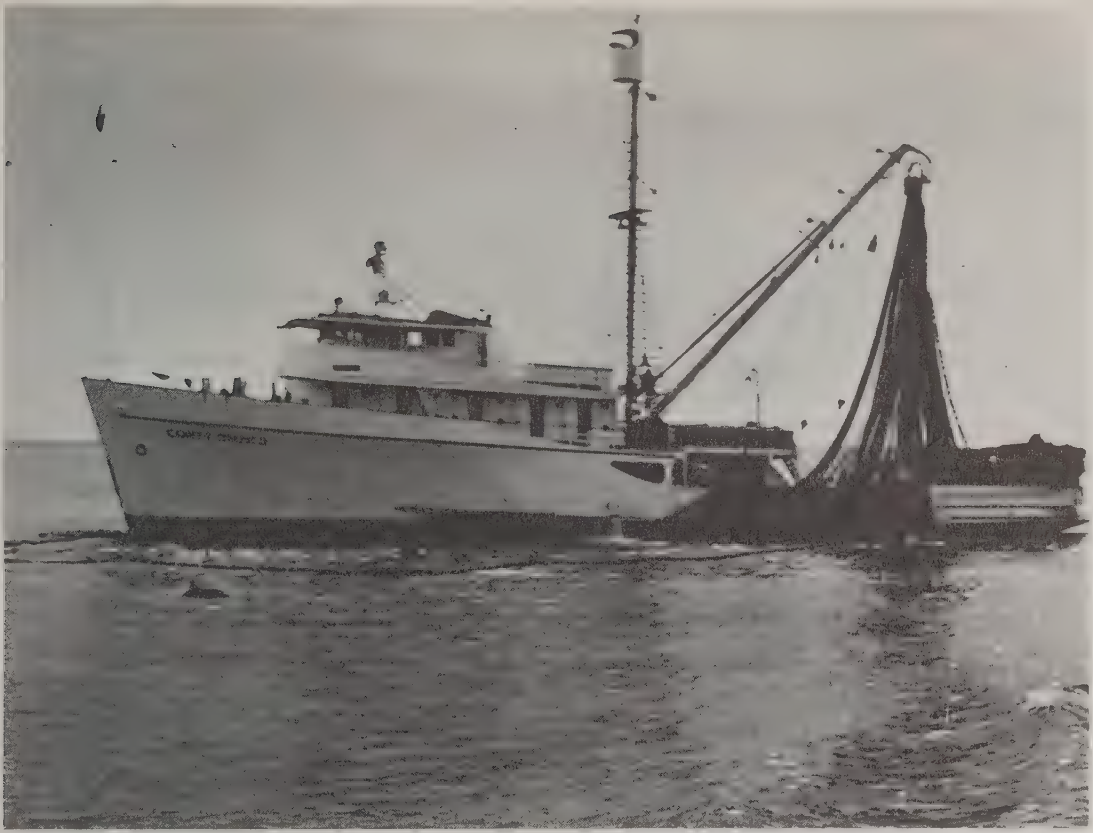
A TUNA SEINER *nears completion of a set. Spotter porpoise (bottom photo) are at the surface and yellowfin tuna are under water in the foreground in a purse seine. When the fish are in the balloon area between the two groups of bunched corks, the porpoise will be spilled over the corkline. (William F. Perrin)*

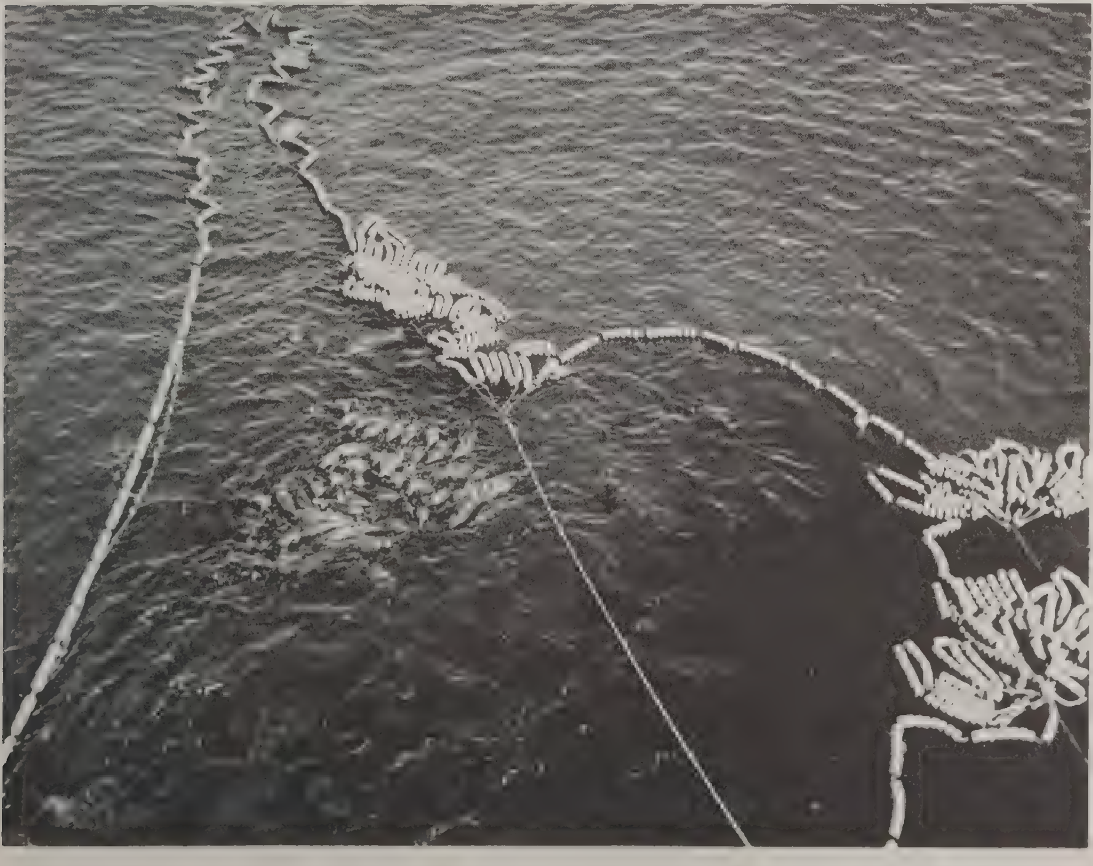
Shark Protection?

Another idea suggested is that the tuna are protected from sharks by their association with porpoise. The supposition is that the porpoise cooperate to drive off sharks, conferring an incidental protective advantage on those tuna which remain close to the school. The protection idea is dramatic but has not as yet been well supported by field observations. In fact, large sharks have been observed to pass unmolested through porpoise herds. Sharks have been seen feeding on porpoise injured during seining operations, but it would seem certain that a healthy porpoise or tuna could easily outswim a shark under normal conditions.

Spatial Orientation?

The association of tuna with porpoise may be analogous to another phenomenon of tuna behavior. Tuna also associate with freely drifting objects, such as logs, seaweed and dead whales. Logs and trees which are disgorged by the rivers of Central America can quickly become gathering points for large numbers of tuna together with other, smaller fishes. Tuna





fishermen take advantage of this association and set their nets around floating objects to catch the fish near them. Sometimes a battery-powered light beacon is attached to a particularly productive piece of flotsam and the boat may follow it for several days, periodically harvesting the tuna. Dr. John Hunter at the U.S. Bureau of Commercial Fisheries, La Jolla, California, recently completed an experimental study of the association of fishes with flotsam in the Pacific off Costa Rica. He concluded that a possible basis for the association is that the floating object furnishes the fish with a visual stimulus for spatial orientation in the optical void of the pelagic environment.

The basis for the tuna-porpoise association may not be as simple or straightforward as suggested by the above hypotheses; it may be mutualistic, of benefit to both animals. Such a relationship, if it exists, will be very difficult to discover and define, but the high value of the tuna tonnage (more than $13 million in 1966) and the possible future value of the porpoise themselves make an attempt to understand the situation necessary. Are the porpoise populations affected by the fishery? Would the fishermen be able to locate the tuna if the porpoise disappeared? Would the tuna populations decline? To answer these questions, we must first solve the mystery of why the tuna and porpoise are found together.

XI/1 1968

The Role of Time-share Computing in Museum Research

JAMES A. PETERS[1]

BRUCE B. COLLETTE[2]

Some of the earliest users of statistics in biology were museum investigators faced with the problems of variation within and between populations and species of plants and animals. The visitor to the research areas of a museum can expect to see desk calculators in almost every laboratory. If he were to check the publications issuing from those laboratories he would find that statistics have played an important role in the decisions made and presented to the scientific community. It would seem, then, that the computer should have been immediately incorporated into museum research because of the ease with which it can handle tasks that would otherwise consume days and weeks of time.

Surprisingly, this has not always been true. Although a few workers have used computers to solve esoteric problems and have widely touted them as panaceas for taxonomic problems, the majority has continued to use desk calculators and has ignored the computer. This neglect of computers has not always resulted from a lack of interest. The magnitude of our problems is one of the reasons why we have hesitated to use computers extensively. We are often involved in the calculations of certain statistical values for comparatively small samples that represent different species, different populations within these species, different sexes within the populations, and different age groups within the sexes. In the analysis of the material we may want to make preliminary comparisons, study the results, re-combine and substitute data on the basis of those results, add new material as it becomes available, and so on. In batch-processing with an off-

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[1] Division of Reptiles and Amphibians, United States National Museum.

[2] Bureau of Commercial Fisheries Ichthyological Laboratory, United States National Museum.

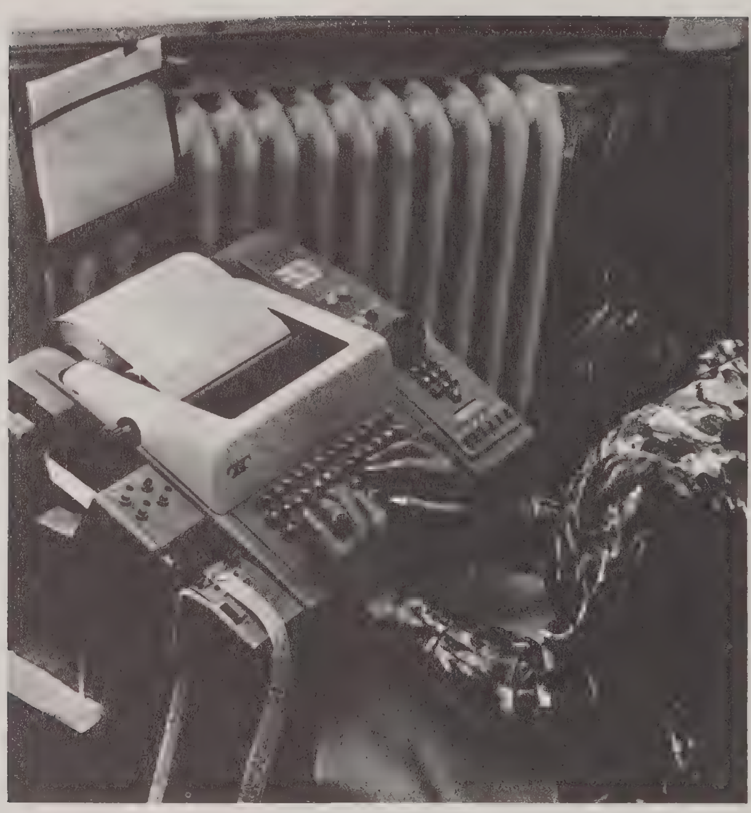


Fig. 1

premises computer, this procedure does not work—or, at least, we did not find it practical. It was much easier to turn repeatedly to the desk calculator which gave us the needed flexibility. Occasionally, when we had large quantities of data for processing, perhaps of such magnitude that the desk calculator became impractical, we turned to the electronic computers, only to find a new source of frustration. Programs for the type of statistics we wished to obtain were seldom available and few programmers were willing to write such unsophisticated programs. On these occasions we shelved problems temporarily, because we could not get the programs written. Finally, the cost of computer services was almost automatically prohibitive to most museum workers, many of whom operate on small maintenance budgets, supplemented when possible by research grants.

Recently, these problems disappeared for the research workers at the

Smithsonian Institution when a teletype connection to a multi-access computer was installed. The teletype is the standard model (Fig. 1) and access to the computer is over the telephone lines. Data and programs can be entered directly on the teletype keyboard or by means of previously prepared paper tape. At the time of writing, three teletypes have been available for six months, and staff use has skyrocketed. The size of a problem is no longer a handicap. We do not hesitate to run the smallest as well as the largest samples. Small samples, that we would never have considered for computer analysis because of the cost, are handled so much more rapidly through time-share computing that the saving in man hours more than offsets the small expense for the time used. Because the data are stored on paper tapes, new material can be quickly added and the analysis run again. The development of time-share computing has brought three major benefits to the research workers at the Smithsonian Institution. First, the time formerly spent on the desk calculator can now be spent on the evaluation of results; second, an increased variety of problems can be undertaken; and third, the value of taxonomic characters can be tested in the course of a study rather than after it has been completed.

To those engaged in research in a museum, the availability of simple languages for programming is perhaps as significant as the time-share facility itself. Scientists at the Smithsonian Institution have been able to learn very rapidly to program in BASIC. Several staff members were already familiar with FORTRAN and ALGOL; for these individuals the transition to time-share computing was virtually instantaneous. For those lacking this background, BASIC has provided an independence of action never previously experienced in our relationships with computer operations. Starting cautiously with simple standard statistical calculations, such as standard deviations and correlation coefficients, we have begun to discover the enormous potentials that lie in time-share computing to release us from some of the more time-consuming museum duties. We have developed a series of programs, many of which use the same format for data input, so that several different analyses can be run with a single paper tape of data. We are moving more and more rapidly in the direction of computer use to solve all kinds of statistical problems encountered in museum research that have previously not been approached in this way. We are beginning to visualize the magnitude of the changes that will result from the widespread use of multi-access computers by museums in the

Fig. 1. The standard teletype as installed in the Smithsonian Institution. No other equipment is needed, since the computer is reached from this machine by telephone line. Data are fed into the computer from the paper tape in the foreground after the tape has been cut by the operator.

United States. This change is perhaps the most exciting possibility.

USE OF TIME-SHARE COMPUTING AT THE SMITHSONIAN INSTITUTION

A review of the various ways in which the multi-access computer is being used at the Smithsonian Institution not only gives some indication of the value of time-sharing there but also shows the diversity of the research being carried on. Utilization of this technique falls into three principal categories at the present time—data processing, data storage and retrieval, and text editing. Future development of several other possible uses is planned.

The first category, data processing, is at present unquestionably the most significant and active area of utilization. Most of the data processed come from studies of the biology of plant and animal species. The comparatively simple analyses are designed to show the existence or absence of differences between samples of different populations. We have used the computer to calculate the series of values (standard deviation, standard error, mean) for Hubbs-Perlmutter diagrams (Fig. 2), that can then be plotted directly from the teletype read-out (Fig. 3). One of us (Collette) is using programs for regression analysis, analysis of co-variance, and plotting of points on graphs in a taxonomic study of the needlefishes. This study provides a basis for distinguishing previously unrecognized populations and species and makes it possible to allocate a newly collected specimen to the proper species by checking its position on a computer-generated graph (Fig. 4).

Maurice E. Salmon, Conservation-Analytical Laboratory, Museum of History and Technology, has written several programs to facilitate data reduction in that laboratory. The first of these deals with the characterization of the spectra of X-ray spectographic tubes. This program involved about two hundred observations per tube spectrum, including the angle of

Fig. 2. Hubbs-Perlmutter diagrams of the number of predorsal scales in five species of the needlefish Strongylura. *The horizontal line represents the range, the vertical line the mean, the black rectangle twice the standard error on each side of the mean, and the open rectangle one standard deviation on each side of the mean. Values are plotted very rapidly from the printout in Fig. 3.*

Fig. 3. Above, a complete program for the calculation of the statistics used in plotting the lines in Fig. 2, and below, the printed results of a run using the data shown in the program, lines 300–301.

Fig. 4. Graph of head width on body length for two populations of Platybelone argalus *from the Atlantic Ocean. Open stars represent specimens from the islands of Annobón and Fernando Póo in the Gulf of Guinea. Closed stars represent western Atlantic specimens. The regression curve is a second degree polynomial based on western Atlantic specimens.*

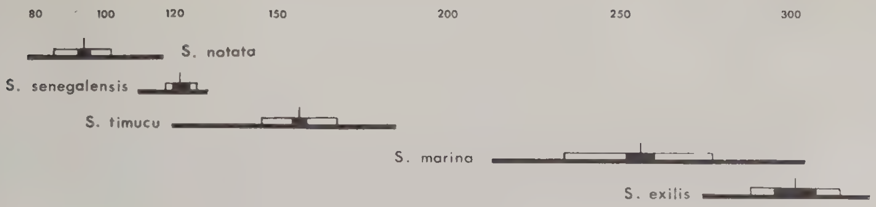
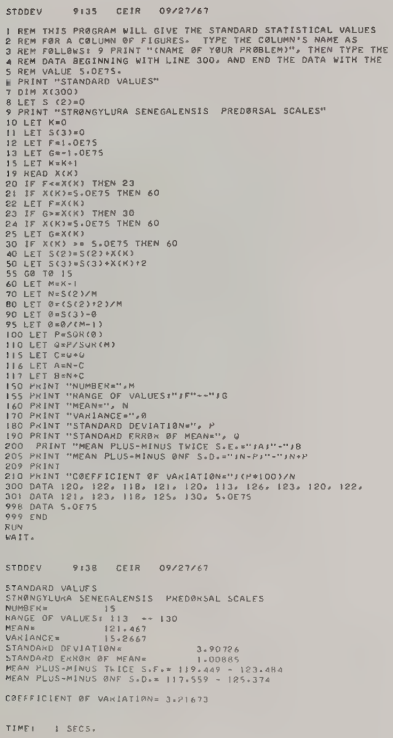


Fig. 2



```
STDDEV     9:35   CEIR   09/27/67

1 REM THIS PRØGRAM WILL GIVE THE STANDARD STATISTICAL VALUES
2 REM FØR A CØLUMN ØF FIGURES.  TYPE THE CØLUMN'S NAME AS
3 REM FØLLØWS: 9 PRINT "(NAME ØF YØUR PRØBLEM)", THEN TYPE THE
4 REM DATA BEGINNING WITH LINE 300, AND END THE DATA WITH THE
5 REM VALUE 5.0E75.
6 PRINT "STANDARD VALUES"
7 DIM X(300)
8 LET S (2)=0
9 PRINT "STRØNGYLURA SENEGALENSIS  PREDØRSAL SCALES"
10 LET K=0
11 LET S(3)=0
12 LET F=1.0E75
13 LET G=-1.0E75
15 LET K=K+1
19 READ X(K)
20 IF F<=X(K) THEN 23
21 IF X(K)=5.0E75 THEN 60
22 LET F=X(K)
23 IF G>=X(K) THEN 30
24 IF X(K)=5.0E75 THEN 60
25 LET G=X(K)
30 IF X(K) >= 5.0E75 THEN 60
40 LET S(2)=S(2)+X(K)
50 LET S(3)=S(3)+X(K)↑2
55 GØ TØ 15
60 LET M=K-1
70 LET N=S(2)/M
80 LET Ø=(S(2)↑2)/M
90 LET Ø=S(3)-Ø
95 LET Ø=Ø/(M-1)
100 LET P=SQR(Ø)
110 LET Q=P/SQR(M)
115 LET C=Q+Q
116 LET A=N-C
117 LET B=N+C
150 PRINT "NUMBER=",M
155 PRINT "RANGE OF VALUES:";F"--";G
160 PRINT "MEAN=", N
170 PRINT "VARIANCE=",Ø
180 PRINT "STANDARD DEVIATIØN=", P
190 PRINT "STANDARD ERRØR ØF MEAN=", Q
200  PRINT "MEAN PLUS-MINUS TWICE S.E.=";A;"-";B
205 PRINT "MEAN PLUS-MINUS ØNF S.D.=";N-P;"-";N+P
209 PRINT
210 PRINT "CØEFFICIENT ØF VARIATIØN=";(P*100)/N
300 DATA 120, 122, 118, 121, 120, 113, 126, 123, 120, 122,
301 DATA 121, 123, 118, 125, 130, 5.0E75
998 DATA 5.0E75
999 END
RUN
WAIT.


STDDEV     9:38   CEIR   09/27/67

STANDARD VALUFS
STRØNGYLURA SENEGALENSIS  PREDØRSAL SCALES
NUMBER=           15
RANGE OF VALUES: 113  -- 130
MEAN=             121.467
VARIANCE=         15.2667
STANDARD DEVIATIØN=              3.90726
STANDARD ERRØR ØF MEAN=          1.00885
MEAN PLUS-MINUS TWICE S.F.= 119.449 - 123.484
MEAN PLUS-MINUS ØNF S.D.= 117.559 - 125.374

CØEFFICIENT ØF VARIATIØN= 3.21673


TIME:   1 SECS.
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Fig. 3

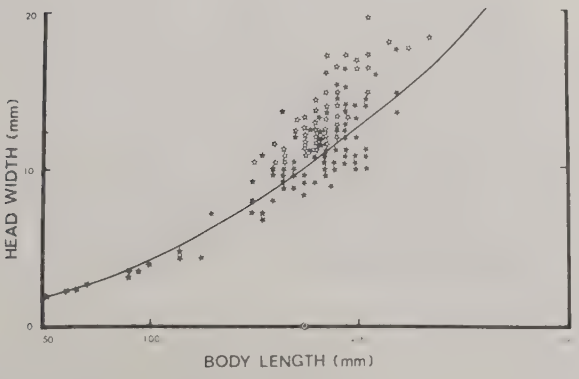

Fig. 4

diffraction, the observed intensity, and the intensity incident on the sample. Salmon calculated that *hand reduction* of the data would require fifty to sixty hours; the time-share computer solution was completed in less than four hours. He developed a second program to determine and apply sets of empirical coefficients to correct quantitative X-ray fluorescence data for matrix effects which involved the solution of n simultaneous equations for n unknowns.

Nicholas Hotton, Division of Vertebrate Paleontology, is analyzing a series of fifty measurements of skeletal parts of recent lizards in the expectation that the information gained, concerning intra- and inter-specific variation, can then be extrapolated to the analysis of large series of dicynodont reptiles collected in South African Permian deposits. Paleontologists are not customarily fortunate enough to uncover fossils in large series, but occasionally they do. Through his analysis Hotton hopes to establish some basis for determining specific limits in fossil reptiles.

W. T. Chase, Research Laboratory, Freer Gallery of Oriental Art, used the computer for weight conversions of 120 Chinese bronze ceremonial vessels. He also used it to calculate the *d*-spacings, from X-ray diffraction measurements taken in a 2-radian powder pattern camera with a program he wrote himself.

Martin A. Buzas, Division of Invertebrate Paleontology, is processing data that consist of proportions that express the relative abundance and diversity of species of Foraminifera[1] in samples from the Arctic to the Gulf of Mexico, by using the Shannon-Weiner information function.

Klaus Rützler, Division of Echinoderms, employs a program that provides information on the zoogeographic similarities and differences between sponge samples.

Henry Setzer, Division of Mammals, uses the computer in the analysis of the mammals of Africa. His work there is supported by a contract with an outside organization because of its significance to the study of the arthropod-borne viruses and their relationship to human infectious diseases.

Ernest A. Lachner and Martin Wiley, Division of Fishes, have used the computer to analyze differences in body proportions and number of breeding tubercles in hybrids and parents of species of minnows.

In addition, many other scientists at the Smithsonian Institution use the time-share service for data reduction.

Data storage and retrieval, the second category of the use of time-share computing at the Smithsonian Institution, is potentially helpful in routine identifications. Scientists in the Museum of Natural History, with its collections of over fifty million specimens of plants and animals from all over the world, are virtually inundated by all kinds of specimens for which identification is required. A similar situation exists, of course, in every large museum. The identification is often a very simple procedure, involving nothing more than a glance by the specialist, whose built-in "computer" he has been cramming with data throughout his professional life. But it is still possible, in many groups of organisms and in many parts of the world, to collect large quantities of material that require many hours of work and study to achieve an accurate identification.

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[1] Foraminifera are one-celled animals whose cast shells are important both in their intrinsic interest to science and as valuable indicator species for oil-bearing layers of the earth.

When such a collection arrives at the museum, a series of events begins culminating in the assignment of a name to each specimen. These events include, first, a review of the literature on the area concerned and the major groups of organisms included; second, the use of "keys," a standard tool for identification, to arrive at tentative names for the specimens; and third, the comparison of the specimens with material already in the collections, and with previously published descriptions to confirm the tentative assignment of a name. Obviously, the first and third steps depend upon access to an adequate library and collection, facilities that have been developed at the Smithsonian Institution over the years.

The assignment of a tentative name, however, is a different matter. If a previous worker has studied either the geographic area or the species concerned, he has probably published data that can be used for this second step. Frequently, either no such work has been published, or, if it has, no keys have been included. Consequently, one must start from the available literature and construct his own identification keys. As a consequence of additional study and publications, published keys go out of date fairly rapidly so that it is difficult to keep up with the changes. Because keys are almost invariably constructed on a dichotomous "either-or" basis, the use of a key is sometimes tedious and one must proceed to an identification from the beginning through a long series of alternatives. The identification procedure appeared to be an area where storage of such sequential information in a computer memory bank, followed by challenge of the memory with data drawn from individual specimens from new collections, might be practical and time-saving. One of us (Peters) decided, therefore, to learn if it might be possible, by the use of BASIC programming, to translate into machine language a standard dichotomous key used in the identification of snakes from Central and South America and permit the computer to select and reject alternatives important in making identifications. It was soon found that the simplest procedure was to permit the computer to select from a series of alternatives rather than from a single pair. Fourteen groups of characteristics useful in the identification of snakes were encoded. With the input of these fourteen encoded items, the computer prints out a generic name in a few seconds of computer time. Occasionally the computer lists two names for genera that could not be distinguished on the basis of the series of fourteen characters. It also prints the additional characters necessary to differentiate between them. In rare instances the machine prints two or more names for which the difficulty of individual recognition is too great for easy encoding in the program. The user must then return to the literature for additional information to determine those genera.

It will be recognized immediately that this new program tends to reduce to a great extent the time and effort spent in the use of keys for identification. If such a computer key is available it also largely reduces the time required for the search of the literature. It should be strongly emphasized, however, that the computer does not in any way relieve the final step—confirming the identification—because any identification obtained from either published or machine keys must always be considered tentative until verified by comparison with descriptions in the literature and previously identified specimens. We might add, parenthetically, that some of the biggest headaches in systematics are derived from investigators who do not follow through on the confirmation step before they publish information based on their use of keys.

The third principal use of multi-access computing at the Smithsonian Institution, text editing, is based on a special program that permits the preparation of text material for review and correction. It incorporates specific printing instructions including such categories as right- and left-hand margin adjustment and justification, centering of headings, indentation, line spacing, and automatic pagination. The BASIC language makes the correction of errors extremely simple, because only the program instruction line containing the error must be retyped and the computer automatically substitutes the corrected line in its proper place. We have used this program to produce letter-perfect copy which is then photolithed for distribution. At present, the only handicap is the teletype itself, because it provides copy only in capital letters. We expect an early solution to this difficulty, however, if in the future it is proven that this is a practical method to produce manuscript material for large-scale reproduction and distribution. The program has already been used to provide material for distribution at lectures on machine programming of systematic keys for specimen identification.

THE FUTURE OF MULTI-ACCESS COMPUTING IN MUSEUMS

As far as we know, the Smithsonian Institution was the first museum in the country with a direct connection to a commercial time-share computer. Very recently, several university museums have installed teletypes and can now communicate directly with the teletype in the Smithsonian Institution. We know of one investigator who tried BASIC programming but found it too restricted for the magnitude of his computer-generated "numerical taxonomy." In our experience, however, most systematists today are not engaged in that level of computer use. On the contrary, many workers use no statistical methods in their taxonomic work have developed a distinct distrust of all computer work because of the extravagant claims made by the proponents of numerical taxonomy. We believe that multi-access computing will serve this group advantageously as well as those workers like ourselves who have devoted many long hours to the computation of measures of distinctiveness between samples.

For the first group it provides a painless introduction to both the computer and to statistics, followed by an easy access to information and data never before used in the analysis of the organisms they are studying and their relationships. For the second group, it means relief from hours and days of labor, plus the opportunity to make some analyses previously considered impractical because of the time required. The reliability and ease of access to the computer, the low cost, and the rapidity with which innovations, equipment, and programs are made available, all combine to make multi-access computing a blessing to research in a museum.

Time-share computing is not, however, an unmixed blessing. We are already beginning to discover some of its shortcomings, including the limitations on the storage capacity of the memory disk; the comparative lack of speed of the teletype in the input of data and output of results; the restriction on the length of any single program, with the attendant limitations on the total amount of data that can be processed in an individual problem; and an occasional busy signal on the teletype line. These problems, we suspect, will be common to all users of multiple-access computers, however, and as a consequence, will be among the first subjects for attack by commercial suppliers who are extremely competitive.

We also expect a comparatively rapid development of computerized keys for identification. The evolutionary sequence that development of this aspect of museum "computerizing" might undergo can be predicted. First of all, it is to be expected that specialists, once they gain access to a time-share computer, will develop computer keys for organisms currently under intensive study. These keys will be tested for accuracy and validity and then translated back into a series of dichotomous choices for publication in revisions or monographs. Since, however, a key submitted for publication immediately begins to go out of date because of continued investigation, the specialist will find it useful to maintain his computer key, inserting corrections and additions as they are published. We expect that workers in other institutions will soon begin to take advantage of the up-to-date information stored in a colleague's computer, by requesting a taped copy of a key for use in their own machines, rather than attempt to use a published and already obsolescent key. Soon, there should be a widespread exchange of computer tapes between museums with compatible systems. This expansion and exchange will result in an over-loading of the memory systems of the computers available to the individual users.

If the exchange should result in a sufficiently large volume of memory bank material, it might then become practical for museums in the United States to consider the formation of a common network, giving all its members access to a mutual store of statistical programs, keys, and other repeatedly used systematic information. Under these conditions, the specialist would continue to maintain the computer key for those organisms he knows best. All other workers would have immediate access to that key by calling it out of the common storage. We also predict that ultimately there will be little purpose to publish storeable systematic information because of its ready availability to workers in an up-to-the-minute state. We even expect that this development may lead to extensive revision in the publication policies of museums in general, in some ways cutting down on the flow of publications and, in others, achieving a general improvement in the quality of the published materials as a consequence of the elimination of repetition. Eventually, field and laboratory data used by taxonomists could be stored in paper tape files (similar to the storage of original data by the American Documentation Institute) and made available in a form ready for computation by anyone who wished to check the results of a previous investigator. The consequences of these changes in mode of action will be far-reaching in the museum world.

Although not part of the computer, the teletype machine and its telephone connections are also significant to research workers in museums. One of the sources of delay in our work today is the necessity for correspondence concerning material in other museums. The completion of a manuscript may be delayed for a month or more while its author awaits a single vital piece of catalogue information or a minor yet important item of data concerning a specimen that requires re-examination by the local curator. The teletype provides transfer of this kind of information in a matter of seconds and facilitates the transmittal of lists of specimens, figures that might be copied incorrectly when received by telephone, and other data. Editors can request that authors verify citations or supply material missing from manuscripts, rather than search out the material themselves or wait for an answer to a letter. Although this aspect of time-share computing can be made available to museums without the computer connection, it is highly unlikely that a network for information transmittal will develop independently of the much more important facet of computer access because most museums will not underwrite the cost of a teletype simply for the time it would save in inter-museum communications. It can be achieved only as a by-product of time-share computing and thus becomes an important aspect of it.

APPROXIMATE COSTS OF TIME-SHARE COMPUTING

Although each contractor has his own method of calculating the charges for the use of the computer, the costs generally tend to average less than $5000 annually. In all systems a standard teletype and connecting line, installed by the local telephone company is used. The teletype and connecting line include a special identifying "dataphone" system, which costs about $50 to $75 per month. Extensions can be attached to this line. Each of these extensions costs about the same as the first machine. Some computer firms charge a flat fee per month. Such a fee includes payment for standard services such as a fixed amount of computer use, memory storage space, and access to the firm's library of standard programs. Any extra use beyond the fixed amounts is added to the basic charge. Other computer firms may charge for the total length of time the user is connected to the system, i.e., the length of the telephone call. In another method, the charge is for the actual time on the computer itself, which is usually measured in seconds. In all methods of billing, however, the basic fee per month is generally $250 to $350, with increasing charges for increasing use.

CONCLUSIONS

It should be clear that we do not share the pessimism concerning time-share computing that has developed in some areas of the computer business and that has been expressed in some recent articles in the computer trade journal, *Datamation*. We have found the facility immensely useful and have high hopes for the future development of the industry and its application to our activities. If the predictions of some supporters of multi-access computing are realized and teletype connections to a central computer become as commonplace in business as the cash register or typewriter, we hope that universities and museums will be found in the forefront in the development, rather than following behind industry and commerce. Our potential uses are likely to be more diverse and manifold than those of the average business. It will be unfortunate if we do not develop them as rapidly as feasible.

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A NET FOR SAMPLING THE INTERTIDAL ZONE OF AN ESTUARY

BY E. J. PULLEN, C. R. MOCK, AND R. D. RINGO

A NET FOR SAMPLING THE INTERTIDAL ZONE OF AN ESTUARY[1]

Our problem was to develop a net for estimating relative abundance of postlarval brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*) in the intertidal zone of Galveston Bay. This zone includes marsh, beach, tidal creek, and tidal flat habitats. The problem was complicated because of the variation in tides, bottom composition, vegetation, and water depth. Allen and Inglis (1958) described a push net and Renfro (1963) described a small beam trawl that can be used in the shore zones to sample small shrimp, but the push net and the beam trawl cannot be fished

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[1] Contribution No. 222, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas 77550.

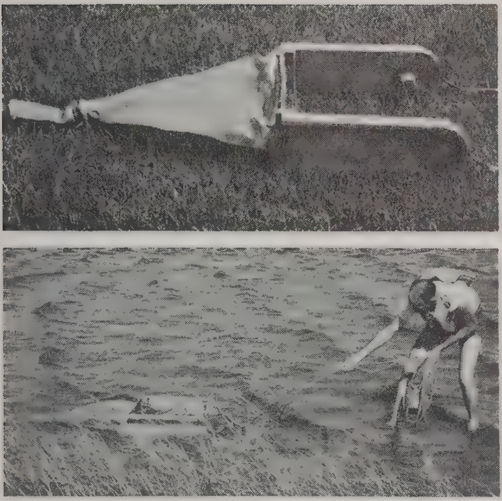

FIG. 1. The marsh net for sampling the intertidal zone of an estuary (upper). The marsh net in operation (lower).

at a constant speed in habitats with soft mud bottoms. This problem was solved by developing a device somewhat similar to a bottom dredge net used by fishermen in the Philippines (Umali 1950).

The sampling device, descriptively called a marsh net, is shown in Fig. 1. The metal frame of the sampler is constructed of No. 22 galvanized sheet metal and ¼-inch (6 mm) welding rods. Frame construction and dimensions are shown in Fig. 2. A 0.5-meter plankton net of nylon monofilament screen is laced to the posterior end of the frame. The net has a bayonet-type cod end for easy removal. The mesh size of the plankton net and cod end is about 1 mm (bar measure). The frame and net weigh 5 kg. Costs were $25 for the metal frame and $23 for the plankton net and cod end.

Collecting procedure was the same in all habitats of the intertidal zone. The net was placed at one end of the sampling area and 30 m of rope was paid out in an arc to prevent the operator from disturbing the sampling site. The net was then retrieved by hand at a rate of about 0.3 m/sec.

The marsh net was successful in capturing small penaeid shrimp in the intertidal zones of Galveston Bay. Catch per 30-m tow often exceeded 100 individuals. The net also caught large numbers of juvenile fish and crabs.

Advantages of the marsh net over the push net described by Allen and Inglis (1958) and the beam trawl described by Renfro (1963) are: 1) the sampling distance does not have to be measured before taking the sample, 2) the net can be

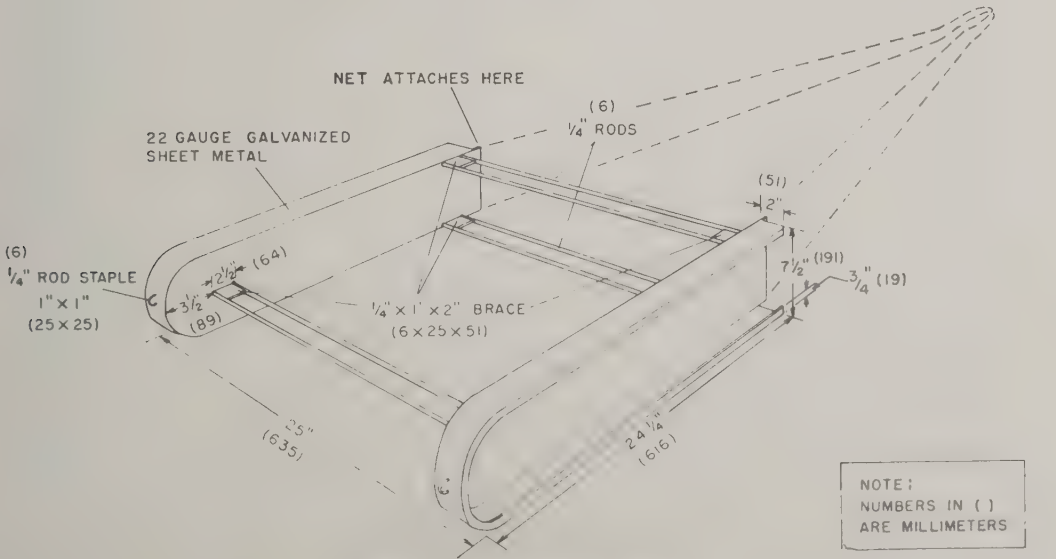

FIG. 2. The marsh net frame

towed at a constant speed more easily, 3) samples can be taken over soft mud bottoms, and 4) sampling is not as tiring to the operator.

E. J. Pullen
C. R. Mock
R. D. Ringo

Bureau of Commercial Fisheries,
Biological Laboratory,
Galveston, Texas 77550.

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New Records of Thirteen Cottoid and Blennioid Fishes for Southeastern Alaska

JAY C. QUAST[1]

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New Records of Thirteen Cottoid and Blennioid Fishes for Southeastern Alaska

JAY C. QUAST[1]

ABSTRACT: Three categories of new records for species of fish are reported: (1) extensions of range eastward or southeastward from the Bering Sea or Gulf of Alaska—*Hexagrammos octogrammus* (Pallas), *Artediellus pacificus* Gilbert, *Triglops metopias* Gilbert and Burke, *Anisarchus medius* (Reinhardt), and *Lumpenus fabricii* (Valenciennes); (2) extensions of range northwestward—*Artedius harringtoni* (Starks), *Oligocottus snyderi* Greeley, *Scorpaènichthys marmoratus* (Ayres), and *Lipariscus nanus* Gilbert; and (3) "fill-ins" for species already reported to the north and south of Southeastern Alaska—*Artedius lateralis* (Girard), *Bothragonus swani* (Steindachner), *Chirolophus nugator* (Jordan and Williams), and *Scytalina cerdale* Jordan and Gilbert.

IN THIS PAPER I bring together distributional data for species that have not previously been recorded from Alaska's southeastern region. The specimens are from the fish collection of the U. S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, and have been obtained principally from activities of the laboratory and the Bureau's Exploratory Fishing and Gear Research Base at Juneau.

For present purposes, Southeastern Alaska is considered to lie between the latitudes of Skagway to the north and Dixon Entrance to the south (Fig. 1). The region, an archipelago composed of marine fjords, has a roughly rectangular outline and is about 590 km long and 176 km wide.

The new records are of three types: (1) eastward range extensions from the Gulf of Alaska or Bering Sea, (2) northwestward range extensions, primarily from British Columbia but also from as far south as Monterey, California, and (3) records that fill gaps for ranges that have been established northwest and southeast of Southeastern Alaska.

Although charts of Southeastern Alaska depict the marine waters as continuous, four lines of evidence suggest that a partial faunal barrier divides the inside waters into northern and southern regions in the vicinity of Kuiu, Kupreanof, and Mitkof islands (Fig. 1). First, water temperatures are usually lower in the northern waters during all seasons than in the southern inside waters or along the outer coast of Southeastern Alaska. Second, five species of shallow-water fishes whose ranges extend into California—*Squalus acanthias, Artedius harringtoni* (records of Auke Bay Laboratory), *Rachochilus vacca, Embiotoca lateralis,* and *Cymatogaster aggregata* (Tarp, 1952)—have been collected in the inside waters south of the Kuiu-Mitkof region but are absent from collections from the inside waters to the north. Third, north and south of the Kuiu-Mitkof vicinity, waters deeper than 10 meters are continuous only via the outer coast. Communication east of the coast is limited to three shallow channels: Dry Strait, which usually bares at low water; Wrangell Narrows, which shallows to about 8 meters; and Keku Strait (Rocky Pass), which shallows to about 3 meters. Fourth, the net flow of surface waters in Frederick Sound, Chatham Strait, and Sumner Strait probably is seaward most of the year because rainfall in the region of the boundary and in the mountains to the eastward is heavy and occurs during all seasons. The rainfall probably creates a net surface flow away from the barrier area, thereby decreasing the opportunities for shallow-water species to reach the three restricted channels of communication.

The new eastward range extensions suggest

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[1] U. S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska 99821. Manuscript received January 8, 1968.

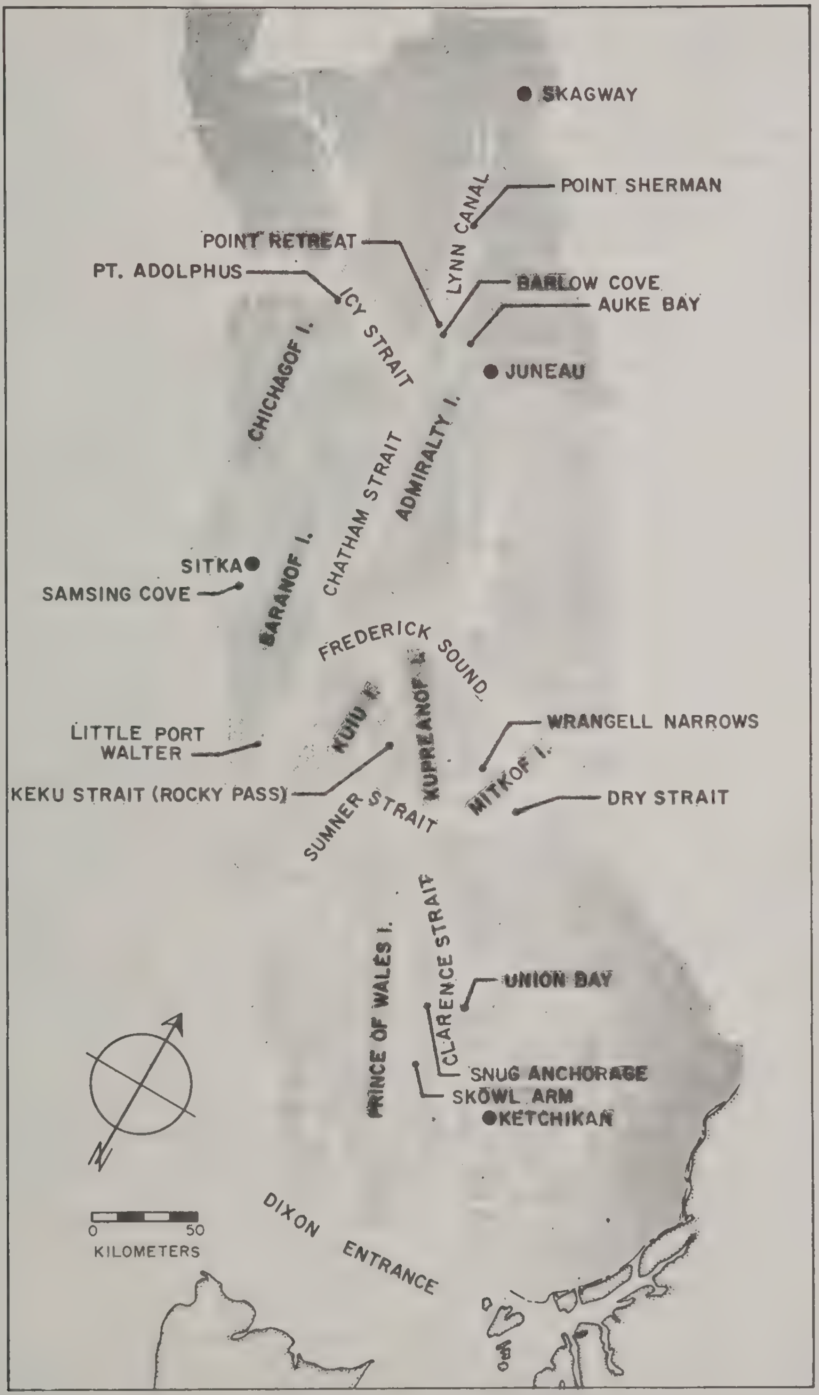
SKAGWAY
POINT SHERMAN
LYNN CANAL
POINT RETREAT
PT. ADOLPHUS
BARLOW COVE
AUKE BAY
ICY STRAIT
JUNEAU
CHICHAGOF I.
ADMIRALTY I.
CHATHAM STRAIT
SITKA
SAMSING COVE
BARANOF I.
FREDERICK SOUND
KUIU I.
KUPREANOF I.
LITTLE PORT WALTER
WRANGELL NARROWS
MITKOF I.
KEKU STRAIT (ROCKY PASS)
DRY STRAIT
SUMNER STRAIT
CLARENCE STRAIT
PRINCE OF WALES I.
UNION BAY
SNUG ANCHORAGE
SKOWL ARM
KETCHIKAN
N
0
50
KILOMETERS
DIXON ENTRANCE

FIG. 1. Map of Southeastern Alaska.

that the northern inside waters of Southeastern Alaska harbor a cold-water enclave of demersal species that has affinities with faunas of the Aleutian Islands, Bering Sea, or regions even farther to the north or west. But any firm conclusion is premature because our collecting methods have not been standardized, numerous critical localities have not been sampled, and available data on distributions are not completely analyzed.

My authorities for species distributions are principally Wilimovsky (1954, 1964), Clemens and Wilby (1961), and Hubbard and Reeder (1965). Although Wilimovsky's "Provisional Keys to the Fishes of Alaska" (1958) is extremely useful for preliminary identifications of the Alaskan fish fauna, the manuscript was given limited distribution and is no longer available (Wilimovsky, personal communication).

Collection numbers for the fish collection of the Auke Bay Laboratory are in the form of two numbers joined by a hyphen and preceded by the letters AB. All lengths are standard.

HEXAGRAMMIDAE

Hexagrammos octogrammus (Pallas)

Two collections: two pelagic-stage juveniles, 43–45 mm, from a salmon trap near Pt. Adolphus, Icy Strait, on 21 June 1955 (AB 55-2); and three specimens, 105–182 mm, taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Wilimovsky (1954) gives the range as the Bering Sea to the Gulf of Alaska, including the Sea of Okhotsk. Quast (1960) gives the range as from northeastern Japan to Yakutat Bay, Alaska. An old record of Bean (1881) gives the locality of "Old Sitka" for "*Hexagrammus* (sic) *ordinatus* (Cope) Bean," a junior synonym of *H. octogrammus* (Quast, 1960).

Evermann and Goldsborough (1907) cite collections of this species made in 1903 from Snug Harbor and Union Bay, Alaska, but the location of these two places is uncertain. The citation suggests the localities of Snug Anchorage and Union Bay, about 65 km northwest of Ketchikan. The fact that both localities in the Ketchikan vicinity are on the cruise track of the U. S. fishery vessel "Albatross" that made collections in 1903 in Southeastern Alaska (deduced from Fassett, 1905) supports the theory that the collections originated near Ketchikan. Correspondence with Robert Kanazawa of the U. S. National Museum discloses, however, that the Snug Harbor specimen originated from the Kodiak Island–Cook Inlet vicinity and that the U. S. National Museum has no specimen of *H. octogrammus* or record of a specimen from a locality named Union Bay. Furthermore, the only locality named Union Bay visited by the "Albatross" on the 1903 cruise was in British Columbia. Very likely, therefore, no collections of this species were made in the Ketchikan vicinity. The southernmost authenticated record is for Sitka.

COTTIDAE

Artediellus pacificus Gilbert

Three collections: one 66-mm specimen taken in a shrimp trawl at 64–75 fathoms (117–137 meters) in the vicinity of the Barren Islands near the mouth of Cook Inlet on 7 August 1963 (AB 64-726); and two collections, 5 and 12 specimens, taken in a shrimp try net over muddy-sand bottom at 50–90 feet (15.2–27.4 meters) in Auke Bay on 25 June 1962 and 27 September 1963 (AB 62-226 and 63-182).

Distribution includes the northern Sea of Japan and Sea of Okhotsk (Schmidt, 1950); the southern Gulf of Anadyr (Andriyashev, 1937); and St. Paul Island (eastern Bering Sea) and Karluk (Kodiak Island) (Jordan and Evermann, 1898). The Auke Bay specimens represent an eastward extension of the range of about 1130 km. Differences in meristic counts between the Auke Bay specimens and those cited by Jordan and Evermann (1898), which are presumably from regions between Kamchatka and Kodiak, do not appear to be important (Table 1).

Artedius harringtoni (Starks)

Numerous collections from Skowl Arm, Prince of Wales Island, taken in shrimp traps fished subtidally; and 56 specimens, 23–80 mm, taken intertidally by divers using rotenone in

TABLE 1

RANGES OF COUNTS FOR *Artediellus pacificus* FROM THREE REGIONS OF THE NORTH PACIFIC OCEAN

ITEM	KAMCHATKA TO KODIAK[1]	COOK INLET (AB 64-726)	AUKE BAY (AB 62-226, 63-182)
Number of specimens	not given	1	17
First dorsal fin	VII–VIII	VII	VII
Second dorsal fin	12–13	12[2]	11–12[2]
Anal fin	11–12	13[2]	11–12[2]
Pectoral fin	22–24	23[3]	21–24[3]
Lateral line pores	22–26	27[4]	21–28[4]
Caudal fin divided rays	9	damaged	7–9[5]

[1] Jordan and Evermann (1898).
[2] Last two rays counted as two elements.
[3] Counts from both left and right fins.
[4] Left side only.
[5] Counts of seven were found only in the smaller specimens.

the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Distribution includes southern California to northern British Columbia (Clemens and Wilby, 1961) and Kodiak Island (Hubbard and Reeder, 1965). Judging from the distributional data, the species probably is common in the southern half of Southeastern Alaska and along nearly the entire outer coast of the region.

Artedius lateralis (Girard)

Common in our collections from coastal and northern and southern inside localities of Southeastern Alaska, including the southern tip of Baranof Island, Sitka, Barlow Cove, and Skowl Arm.

Clemens and Wilby (1961) give the distribution as southern California to the Queen Charlotte Islands, and Hubbard and Reeder (1965) report the species from Kodiak Island. Hubbard and Reeder also suggest that the name *Artedius delacyi* Hubbs and Schultz applies to the species described as *A. lateralis.* The type description of *A. delacyi* states that the species, based on specimens from Kodiak Island, is very closely related to *A. lateralis* (Hubbs and Schultz, 1941). Comparisons of critical proportions of our specimens from Sitka with those from the type description of *A. delacyi* Hubbs and Schultz also support the argument against the distinctiveness of *A. delacyi* (Table 2). The main distinguishing characteristic of *A. delacyi* in the type description involves thickness of the lips, a feature that probably varies according to the conditions of preservation.

Oligocottus snyderi Greeley

Three specimens, 37–57 mm, taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Distribution of the species according to Clemens and Wilby (1961) is from southern California to the Queen Charlotte Islands. Our collection is the first recorded from Alaska and extends the known range northward about 340 km.

TABLE 2

CRITICAL PROPORTIONS OF *Artedius delacyi* AND *A. lateralis* PRESENTED BY HUBBS AND SCHULTZ (1941) AND OF SITKA SPECIMENS OF *A. lateralis* FROM THE AUKE BAY LABORATORY COLLECTION

SPECIES	NUMBER	UPPER LIP WIDTH[1] ÷ LEAST SUBORBITAL WIDTH	LEAST WIDTH OF LIPS[2] ÷ LEAST SUBORBITAL WIDTH	HEAD INTO STANDARD LENGTH
A. delacyi	3	ca. 1.0	ca. 1.0	2.75–2.85
A. lateralis from Sitka	10	0.7–1.0	0.7–1.1	2.52–2.71
A. lateralis	([3])	0.6–0.8	0.6–0.8	2.50–2.80 (usually 2.60–2.70)

[1] Measured sagitally.
[2] Least width of both lips below suborbital.
[3] Not given.

Scorpaenichthys marmoratus (Ayres)

One 93-mm specimen taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

According to Clemens and Wilby (1961) the distribution is from southern California to northern British Colombia, and individuals are common in the Queen Charlotte Islands. Our collection is the first recorded from Alaska and extends the known range northward about 340 km.

Triglops metopias Gilbert and Burke

One 119-mm specimen taken in a shrimp try net on a silty-sand bottom at approximately 51 feet (15.5 meters) in Auke Bay, 27 September 1963 (AB 63-182). Wilimovsky (1954) gives the distribution as Bering Sea, and later (1964) reports it from Amchitka Island and the Semisopochnoi Island-Petrel Bank vicinity. The Auke Bay Laboratory also has collections from near the Shumagin Islands.

The Auke Bay specimen resembles those, including the type, described from the Bering Sea by Gilbert and Burke (1912), but has counts that are one or two units, depending on the character, below the ranges cited for rays of the soft dorsal, anal, and pectoral fins and for scutes along the lateral line; it also has 21 dorsal scutes as compared with "26 or 27" in the type. The record for Auke Bay is the first for the species in the eastern Gulf of Alaska and extends the known range eastward about 2900 km.

AGONIDAE

Bothragonus swani (Steindachner)

One 51-mm specimen taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Clemens and Wilby (1961) give the range as California to the Queen Charlotte Islands, and Hubbard and Reeder (1965) report the species from Kodiak Island.

LIPARIDIDAE

Lipariscus nanus Gilbert

Four specimens, 26–32 mm, taken in three collections made with an Isaac-Kidd trawl at night at 100 meters in Lynn Canal. Two collections (AB 64-63, AB 64-999) are from near Point Sherman, and one (AB 64-72) is from near Point Retreat.

Gilbert (1915) obtained five specimens, including the type, from Monterey Bay, California. The Lynn Canal collections represent a northward extension of range of about 2600 km.

STICHAEIDAE

Anisarchus medius (Reinhardt)

The species was formerly in the genus *Lumpenus* Reinhardt, but Makushok (1958) places it in *Anisarchus* Gill. The Auke Bay Laboratory has several collections from the Gulf of Alaska and the Aleutian Islands, and one collection of 54 specimens, 59–117 mm, taken in a shrimp trawl at 60–90 fathoms (32.8–49.2 meters) in Auke Bay on 25 June 1962 (AB 62-226).

Wilimovsky (1954) gives the range of the species as "Arctic Alaska-Bering Sea; North Atlantic Ocean"; Andriyashev (1954) states that the species is circumpolar and occurs in the Sea of Okhotsk and the northern Sea of Japan. The Auke Bay collection extends the known range eastward about 1400 km.

Chirolophus nugator (Jordan and Williams)

One 57-mm specimen taken intertidally by divers using rotenone in the vicinity of Samsing Cove, near Sitka, on 18 March 1964 (AB 64-954).

Clemens and Wilby (1961) give the range as from northern California to the Strait of Georgia. Hubbard and Reeder (1965) report the species from Kodiak Island.

Lumpenus fabricii (Valenciennes)

One 215-mm specimen captured by hand on a beach at low tide at Auke Bay on 1 December 1963 (AB 63-234). The Auke Bay Laboratory also has one 255-mm specimen from Kachemak Bay, Cook Inlet (AB 64-738).

Andriyashev (1954) lists the species as amphiboreal and occurring in the Chukchi Sea and the northern Sea of Japan; Wilimovsky (1954) gives the range as "Arctic Alaska-Bering Sea; North Atlantic Ocean."

Scytalina cerdale Jordan and Gilbert

Five specimens, 49–64 mm, taken by hand on a beach at low tide in the vicinity of Little Port Walter on Baranof Island on 13 May 1960 (AB 63-32).

This species has been recorded from the Bering Sea to California (Wilimovsky, 1954), and on Agattu Island in the Aleutian Chain (Wilimovsky, 1964).

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4. SOME PHYSICAL ASPECTS OF THE INSHORE ENVIRONMENT, PARTICULARLY AS IT AFFECTS KELP-BED FISHES

JAY C. QUAST
U.S. Bureau of Commercial Fisheries
Auke Bay, Alaska

INTRODUCTION

The kelp beds of southern California are named for the dominant algal species, *Macrocystis pyrifera,* which comprises all but a very small fraction of the floral standing crop in alongshore areas. Not only is a rich fish fauna associated with the kelp beds, but kelp itself has economic value, particularly for alginic acid and food additives. From 1950 to 1960 many dense beds of kelp seriously declined along the coast of southern California and Baja California. The thinning or occasional outright disappearance, was presumed to cause losses of the resident sportfishes, alarming sportfishing, conservation, and commercial interests. This alarm resulted in several successive research programs at the Scripps Institution of Oceanography, La Jolla, to expand general knowledge of kelp beds and their ecology. A 5½-year study by the late Conrad Limbaugh surveyed the biology of kelp beds and their fauna (Limbaugh, 1955). In July 1956, the Institute of Marine Resources of the University of California undertook a 5-year study of the biology of kelp and the associated fishes and invertebrates. This study, known henceforth as the Kelp Program, utilized specialists in botany, bacteriology, fisheries biology, ichthyology, biochemistry, and invertebrate zoology. Although administered and supported in part by the University of California, San Diego, basic support was derived from the California Department of Fish and Game.

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Editing and helpful criticism were furnished by Carl L. Hubbs and Wheeler J. North. The late Conrad Limbaugh, an excellent SCUBA diver and biologist gave SCUBA instruction, and furnished invaluable counsel on the biology of kelp beds and their fauna. Diving technicians of the Kelp Program, particularly Jean Kauanui, James R. Stewart, and Earle G. Cunnison, also played an essential role in the research. The manuscript was typed by Lois I. Rushing.

THE KELP ENVIRONMENT

The kelp [1] plant (Figure 10) grows from an anchoring structure, the holdfast, which is usually attached to a rocky substrate. The plant extends to the surface, where the buoyant fronds may spread horizontally for 20 feet or more. These floating fronds form a canopy, which, like the upper foliage of terrestrial plants, shades the regions below.

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[1] The unmodified term "kelp" will henceforth indicate the genus *Macrocystis*.

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Fish Bulletin 139, 1968.

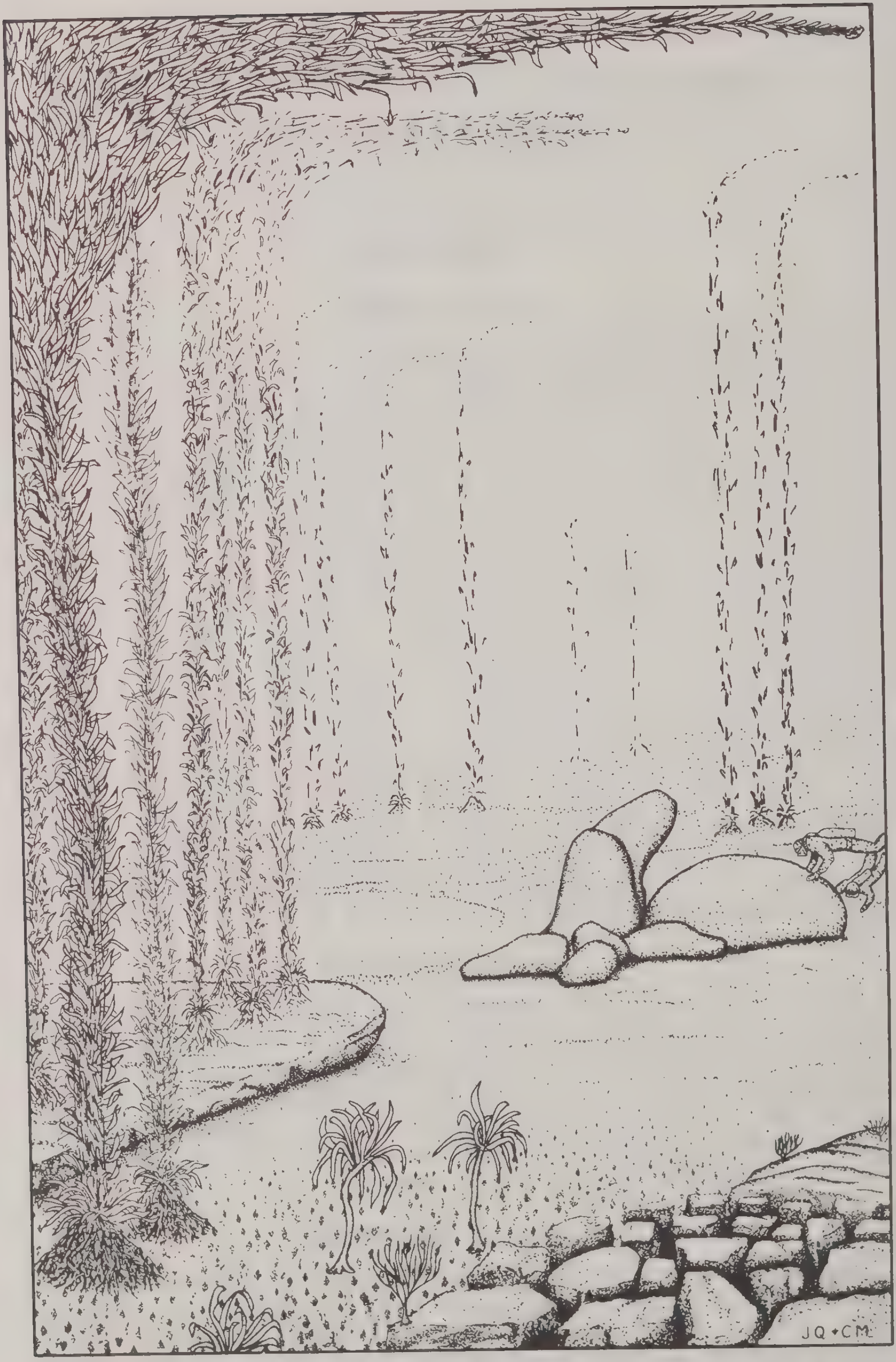

FIGURE 10. Drawing of a representative kelp bed of the San Diego region. The rock formations depicted are fragmented rock (right foreground), pavement rock (center), a ledge (left center), and boulders (right background). Plants include columns of kelp *(Macrocystis pyrifera)*, the 2–4-foot *Pterygophora californica* (or the similar *Eisenia arborea)* and a short (2–4 inches) tufted coralline algae that clothes the pavement rock (center). A 1-foot gorgonian is represented on the fragmented rock (right foreground). Two divers are included for scale (right background). No fish are represented. A sand patch, common in some areas, is shown in the left background, behind the ledge.

Although kelp usually occurs on rocks it also attaches to ropes, cables, pier pilings, and metal objects. In a protected environment, such as the Santa Barbara region, it may occur on a sand bottom. Relatively calm conditions exist here because a westerly trending coastline and a chain of offshore islands damp the prevailing west and northwest swells.

Kelp beds typically extend from quite shallow water (*ca.* 20 feet) to 80 feet or more. At the shallow limit giant kelp intergrades with and is replaced by feather boa kelp, *Egregia laevigata*; at the deeper margin it typically is replaced by bull kelp, *Pelagophycus porra,* after a zone of intergradation. Whether one or more species of *Macrocystis* occur in southern California is uncertain. Some specialists classify the kelp north of Palos Verdes, near Los Angeles, as *M. angustifolia.* Any species differences have slight or negligible effects on the environment of fishes.

Under water, kelp beds typically resemble forests with nearly complete canopies (Figure 10). Tangled columns arise from conical holdfasts which are topped with clumps of sporophylls. Holdfast size generally increases with age. Although the holdfast is perennial, maximum life of the stipes is usually 6 months, possibly extending to 8 or 9 months under the best growing conditions (*cf.* North, 1961). Usual diameter of kelp holdfasts near La Jolla is between 10 inches and 2 feet. Holdfasts contain characteristic aggregations of invertebrates (Ghelardi, 1960) as well as fishes (discussed in succeeding sections). Kelp-bed substrates will be divided into three categories, representing subjective estimates of their physical relief. ''Low relief'' includes sand, silt, or pavement rock bottom or combinations thereof. These are regions with few macroscopic holes for fish or invertebrate refuge. ''High relief'' refers to bottoms with large exposed rock surface per unit area. Examples are boulder piles, cobbles, boulder-cobble flooring with a high interstitial volume, and solid rock terrains with numerous crevices, cliffs, projecting shelves, ledges, or rotten or honeycombed rock. ''Moderate relief'' applies to intermediate conditions such as pavement-rock areas with isolated rock piles, depicted in Figure 10, or rocky areas with a slightly broken substrate.

TEMPERATURE

In shallow inshore waters the temperature structure generally grades from well-developed vertical stratification during summer and fall to nearly isothermal conditions in winter and spring. Surface temperatures are normally coldest from January to March but minimum temperatures at 100 feet normally occur in May and June (Figure 11). This lag in the cooling of deeper waters was suggested by Leipper (1955) and was verified by diving observations during the Kelp Program. Maximum temperature stratification occurs between June, the month of lowest temperatures at 100 feet, and August, the month of maximum surface temperatures. Such a temperature sequence characterizes regions of upwelling (Sverdrup, Johnson, and Fleming, 1942). Cooler water is brought near the surface from February through June by strong northwest winds that are frequent along the coast of the Californias at this time of year (a wind-induced ocean

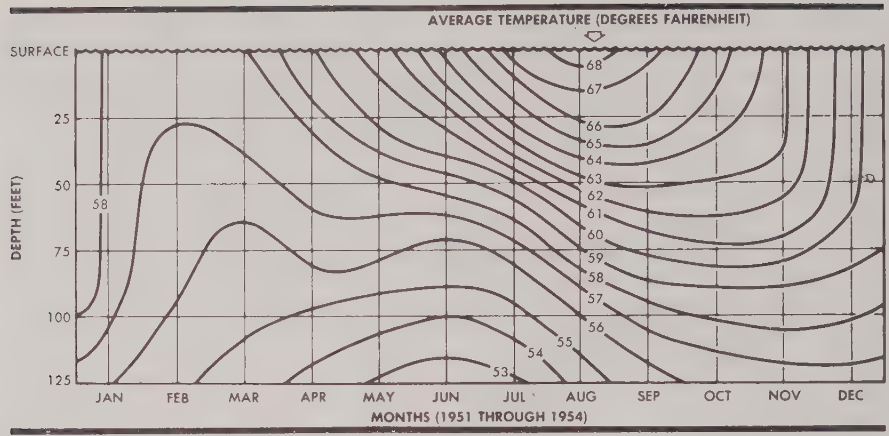

FIGURE 11. Average water temperature off La Jolla (MLR Sta. 93, 30 nautical miles offshore) during 1951–1954. The bottom water (100-feet) was coldest in June and the surface was warmest in August, with an intervening period of highest stratification. Upper part of column was nearly isothermal from November through January (Diagram furnished by Mrs. Margaret K. Robinson, Division of Marine Resources, Scripps Institution of Oceanography).

current moves at 45° to the right of the wind direction). Highest geostrophic wind velocities occur in June for coastal regions and in July for offshore regions (Eber and Sette, 1959). Leipper (1955) postulates that inshore isotherms rise during spring because cold upwelled water originating near Point Conception moves southward. Additional local upwelling at various points south of Point Conception is implied by Sverdrup, Johnson, and Fleming (1942). Narrow bands of cold water occur along the coast of Baja California south of projecting points or headlands, due to local upwelling (Leipper, *l.c.*). This phenomenon has been well documented by temperature records collected for more than a decade by Prof. Carl L. Hubbs of the Scripps Institution of Oceanography (unpublished).

Although inshore waters display well-developed temperature stratification during summer and early fall, temperature stability is poor during these seasons insofar as the biota is concerned. Tidal excursion (up to 6 feet in the San Diego region) may subject attached inshore animals to daily fluctuations of several degrees Fahrenheit. Much greater temperature fluctuations have been measured at fixed points during this season of temperature stratification and are attributable to at least two causes: (i) internal waves moving toward shore beneath the ocean surface and (ii) short-term local upwelling from sporadic offshore or northerly winds.

LaFond (1959) demonstrated that nearly all longitudinal surface slicks off Mission Beach, San Diego, are associated with internal waves. Beneath and slightly behind each slick the isotherms plunged bottomward (Figure 12). Although no data were presented on the frequency of such slicks from day to day, they are of nearly daily occurrence during the summer and fall months (La Fond, *l.c.*). Average shoreward speed was 0.31 knots, with a frequency of one to nine waves per hour. An analysis of the depth distribution of the isotherms in LaFond's figures showed that the greatest temperature fluctuations en-

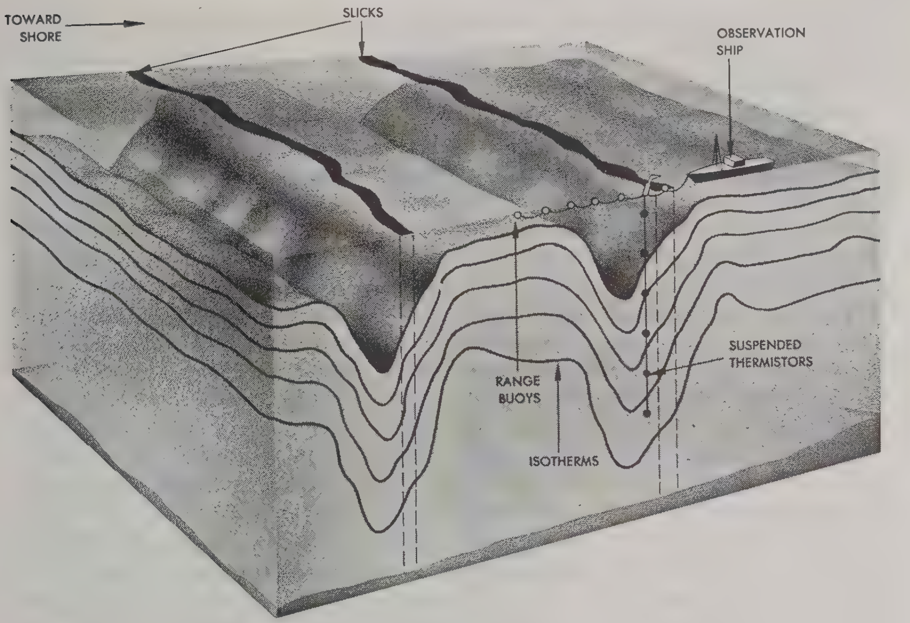
TOWARD SHORE
SLICKS
OBSERVATION SHIP
SUSPENDED THERMISTORS
RANGE BUOYS
ISOTHERMS

FIGURE 12. Three-dimensional representation of internal waves in the inshore waters off Mission Beach, San Diego. (From LaFond, 1959.)

countered by a fixed biota occur well below the surface (Figure 13). This region of temperature fluctuations descends at least to 30 feet, the greatest depth measured by LaFond, and undoubtedly penetrates much deeper. For example, during measurements on 12 June 1958, the maximum fluctuations of 11.4° F. occurred at 20 feet, during seven

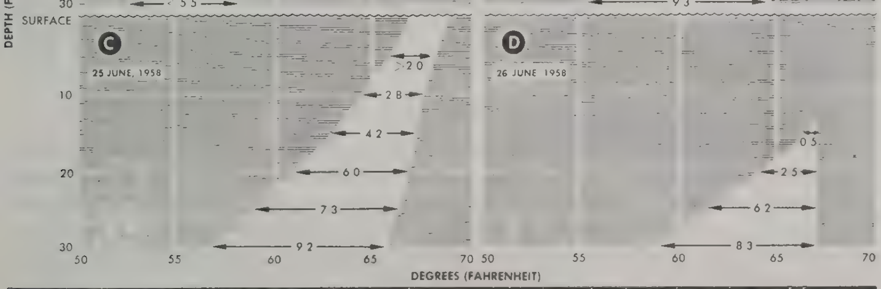

FIGURE 13. Examples of hypothetical temperature excursions with depth for kelp beds of the San Diego region in June. (Calculated from LaFond, 1959.)

slicks, in contrast to a 4-degree difference at 5 feet and 5.5 degrees at 30 feet (Figure 13A). On 24 June the region of maximum temperature change (9.4 degrees) was near 25 feet and the eurythermal zone obviously extended much deeper, with 14 slicks occurring in 4 hours and 45 minutes (Figure 13B). On June 25 the eurythermal zone extended to the surface; however, the maximum temperature oscillation (9.2° F.) was probably below the deepest measurement (Figure 13C). Similarly, on 26 June the eurythermal zone apparently reached its greatest dispersion (8.3° F.) at depths greater than the maximum surveyed, and the surface 14 feet were isothermal (Figure 13D).

Temperature elevations occasionally develop in normally cold, upwelling areas south of projecting headlands, down to considerable depths. Westerly winds maintain the upwelling process during summer but occasional storms accompanied by strong southerly or southwesterly winds could theoretically ''pile up'' warm surface waters to depths of 100 feet or more in these normally cold regions. Although this mechanism has not actually been witnessed, it offers a reasonable explanation for sudden disappearances of kelp from the southwest side of Punta Banda, Baja California, during the fall of 1957 and again in 1959. A surprising scarcity of fishes was also found in the area in June, 1960. High standing crops had been measured previously by wall-net collections and underwater transects (described in following chapters).

WAVE ACTION

One of the striking features of kelp-bed environments on open coasts is the reversing horizontal water movement or ''surge'' caused by heavy swells. It is normally present from the surf zone to depths of 30 feet or more. Frequently it extends to 60 feet, with estimated horizontal transits of 6 to 10 feet by suspended bottom materials. Occasionally divers experience slight surge at 100 feet, particularly during times of long-period swell.

Such water motion appears to have profound effects upon the biology of the rocky-shore environment. Particles of shell and sand may be lifted 5 to 10 feet off the bottom at 60 feet by the turbulence and kelp plants are subjected to strong lateral forces. Divers may need to cling to bottom objects to accomplish work, and fishes must swim rapidly in alternate directions to remain within a small area. Turbulence sweeping irregular bottom features appears to create important feeding regions for fishes. Schools of *Chromis punctipinnis* typically feed about or above prominences on the bottom. At least during spring, kelp bass and sheephead are more abundant near bottom features of high relief.

VISIBILITY

The importance of visibility for food getting and protection in fishes is easily judged on *a priori* grounds, and observations offer convincing evidence that water clarity is extremely important in the lives of the majority of the fish species. Clarity of rocky-shore environments is subject to considerable daily, weekly, and seasonal variations. Likewise a single area may sometimes vary considerably from hour to hour and frequently differs between surface and bottom. Usually, however, visibility remains fairly constant for periods of weeks or more.

Three factors regulate visibility importantly: (i) bottom disturbance due to surge, (ii) plankton blooms, and (iii) water-exchange. Wave action may cause considerable turbulence near the bottom down to 60 feet, particularly during long-period swell. At such times, bottom visibilities are typically reduced to 10 feet or less. Intense turbidity may occur only in the lower 6 to 10 feet of the water column, particularly during times of long-period swells in calm weather. Concentrations of fishes normally occur near the bottom, but under these conditions the turbid layer may be nearly devoid of fish (even when allowance is made for the restricted visibility). If kelp is present, fishes such as the kelp bass and kelp rockfish under such conditions are much more abundant in the upper, clearer waters.

High plankton density frequently causes poor visibility in inshore waters at La Jolla, especially during the summer months. Although dense plankton layers are usually no more than 10 to 15 feet deep, they occasionally extend down 100 feet or more, allowing only 4- to 5-foot visibility. An example was noted by the writer during a dive on 25 July 1960 near the Scripps Institution of Oceanography with the diving officer James R. Stewart:

> "The first dive was made at approximately 1 PM in the Scripps Submarine Canyon. Patches of red tide (*Gonyaulax polyhedra*) were visible at the surface, however, we expected that the turbid zone would not extend more than 10–15 feet below the surface, or 30 feet at most. However, as we went down the anchor line (which went straight down because the small anchor had slipped off the canyon wall) we noticed no clearing of the water. Visibility decreased and the illumination rapidly dimmed. Finally at approximately 115 foot depth Jimmy stopped and signaled that we might as well go up again. I agreed as I could barely see him (he was at a distance of approximately 2 feet)—it was like diving into a pot of ink."

Usually the lower boundary of a surface turbid layer is characterized by a dramatic improvement in visibility and a sudden temperature drop. It is possible that the exceptional deep concentration of plankton noted above resulted from diving by chance in the surface-convergent part of an internal wave. As noted previously, the surface layer may extend to considerable depths at such times.

Inshore waters occasionally become very clear off La Jolla and San Diego. The bottom may be visible from the surface to depths of 30 feet or more. If ocean temperatures drop simultaneously, upwelling may have caused the clear water. If there is no considerable drop in temperature, a mass of clear oceanic water may have been carried into the shallow water zone.

Poor underwater visibility is not necessarily associated with the stormy half of the year and its periods of rough water. Two years of diving observations around San Diego disclosed that visibilities on and near the bottom averaged better during the rough-water season than for the calm half of the year (Figure 14). Good visibility (25–30 feet) was recorded several times within a day or two after the passage of a storm front and the strong northwest winds and rough water associated with the second half. It is not known if suspended materials settled rapidly, or if turbid water was replaced by oceanic or upwelled water.

Routine observations during the relatively calm summer and fall seasons indicated that visibility is usually better for surface and midwater regions than near the bottom (Figure 14). This is not true in summer when heavy plankton blooms cause very poor visibility near the surface. More uniform visibility throughout the water column during winter and spring may result from storms, long-period swells, and weak stratification. Clear oceanic water lies close to the coast near San Diego. Good visibilities characterize the Coronado Islands, Baja California only 8 nautical miles off the coast (Figure 14).

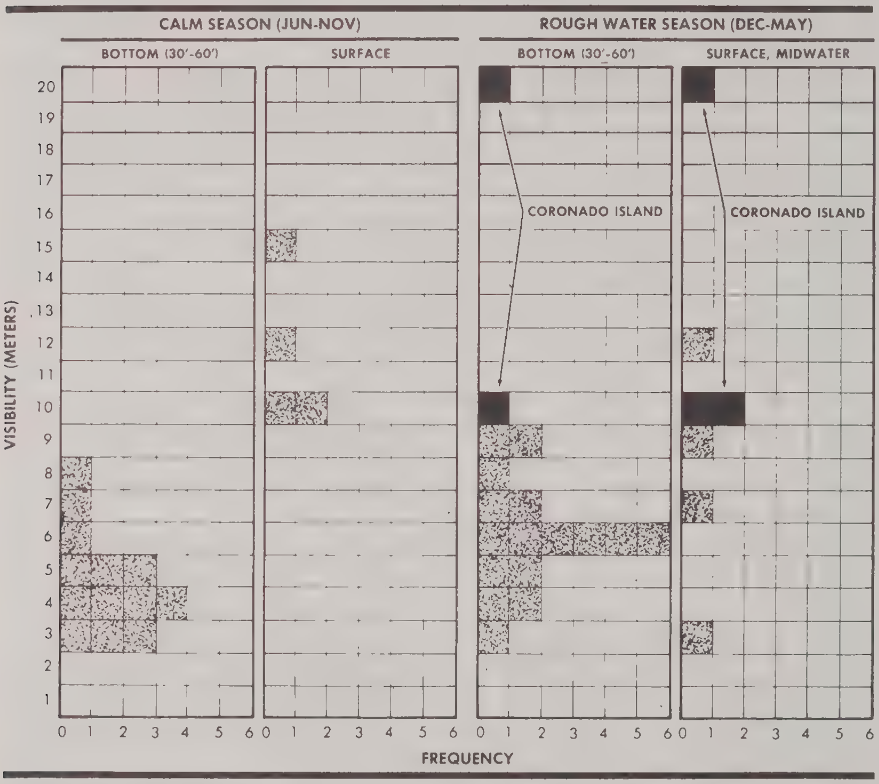

FIGURE 14. Frequency of visibility distances that were encountered underwater during a year of dives in the San Diego region. Shaded areas represent inshore waters; and the solid areas offshore waters near the Coronados Islands, Baja California, Mexico.

DISCUSSION

These important physical factors of the kelp-bed environment are presented as background for succeeding chapters on the kelp-bed fishes. Undoubtedly they play a very important role in the biology of the kelp beds and their fauna, but detailed studies of amplitudes and effects were beyond the resources of the Kelp Program.

In general terms, two rocky-bottom habitats are apparent to the SCUBA diver in the San Diego region. A shallow subtidal zone is de-limited from the deep habitat approximately by the 100-foot depth contour. The shallow region is subject to surge and currents, to considerable daily and seasonal temperature fluctuations, and, in some localities, to moving sediments and poor visibilities. In the San Diego region, this zone has a reasonably well-defined demersal fish fauna which may be called the rocky-inshore fauna. The zone and fauna correspond loosely to the inner sublittoral zone and fauna of Hedgpeth (1957). The lower depth boundary varies with local conditions of wave exposure, substrate character, and water clarity. The dominant fishes usually range throughout the zone and considerably deeper, apparently disregarding bottom composition and temperature. These species, which include the kelp bass, California sheephead, and kelp perch, usually show no clear-cut bathymetric distributions relative to strong thermoclines in shallow water. This apparent disregard for temperature contrasts indicates that these fishes are probably adapted to a thermally unstable environment and are relatively unaffected by such changes. Numerous causes of temperature differences in the inshore region are identifiable. Differences may be associated with coastal configuration and wind direction: Because the prevailing winds of southern California and Baja California are from the northwest, warm water tends to accumulate on the north side of headlands and cold water upwells on the south side. Reversals occur during prolonged southerly gales that sometimes accompany storms. Internal waves caused significant short-term temperature fluctuations in the inshore zone. The fauna apparently tolerates these changes rather than moving considerable vertical or horizontal distances to maintain an isothermal environment. Temperatures of the upper and lower regions of the inshore zone also vary seasonally, but in nearly opposite directions: Surface layers are usually warmest between mid-summer and mid-fall and coldest in winter, whereas at 100 feet temperatures are usually lowest at the beginning of summer and highest in fall.

Although its effects have not been assessed, surge influences the inshore environment profoundly, and is undoubtedly important to fishes. Water clarity is also very important and seems to regulate the volume of water available for foraging by many species (a point discussed more fully in succeeding chapters).

Below the inshore zone physical conditions appear to be much more stable. The shallow-water fauna diminishes and cold-water species appear. The effects of physical factors outlined above decrease. Fleshy algae become scarce, presumably due to the low levels of illumination. Cover for demersal fish species is limited to isolated areas of rock, in places abundantly covered with attached gorgonians. A more northern fish fauna appears here. The bathymetric range of this fauna actually extends into the intertidal where upwelling is nearly continuous, and extends shoreward considerably during temporary shallow incursions of colder water.

SUMMARY

1. General physical aspects of southern California kelp beds influence the fishes importantly.
2. Kelp beds of southern California and the Pacific coast of Baja California normally occur on rock. Some beds of the Santa Barbara region, however, grow on sand and mud.

3. Surface and bottom water temperatures differ most during summer, particularly in July, when the surface water is nearly at its highest temperature and the bottom water is nearly at its lowest.

4. Large fluctuations in water temperature, with a period of less than 1 hour, are believed to occur in kelp beds at mid-depths during summer and early fall months. Fluctuations of 11° F. apparently are not extreme, and some temperature fluctuations penetrate at least to the depth of 60 feet.

5. Temperature fluctuations with periods greater than 1 hour but less than seasonal, are attributed to local currents, upwelling, and incursions of oceanic water.

6. Wave action in the San Diego region extends to depths of 60 feet, occasionally deeper, and is important to many organisms.

7. Observed seasonal differences in underwater visibility may be attributed to several causes.

8. The lower boundary of the inshore environment in the San Diego region is approximately 100 feet deep. Shallower depths are characterized by high levels of illumination, fleshy algae, a distinctive fish fauna, warmer temperatures than the deeper layers, marked temperature fluctuations during the summer and fall, heavy and frequent surge, and, generally, by poor visibility near the bottom.

References for this paper follow reprint no. 131
in this volume.

The data show no discernible differences when areas of heavy and light fishing were compared, probably because sheephead are taken infrequently in the sportfish catch relative to other species. Density estimates for regions classified by kelp density showed a slightly higher average for moderate-dense kelp but the values are of questionable significance (Table 17). The large variance for regions with moderate to heavy kelp was chiefly due to single transects made at Papalote Bay and Turtle Bay, where other diving operations immediately preceded the fish census. Probably the disturbance caused an influx of fish into the transect area prior to the census. An overall value of 14 adults per acre (as for the La Jolla transect site) might be a more reasonable

TABLE 17

Density Estimates of Sheephead in Areas of Low and High Kelp Density. Out and In Counts Averaged for Each Transect

Site and classification	N	Range (adults per acre)
Kelp none to light (25 transects)		
Bird Rock, La Jolla, and La Jolla transect site*	4	5–24
Coronado Island, Mexico (South Island)	1	2
Guadalupe Island, Mexico	4	6–10
Summary: mean = 10, variance = 45.25		
Kelp moderate to heavy (16 transects)†		
Bathtub Rock	3	3–4
Bird Rock (sites other than above)	2	5–6
Point Loma	4	0–9
Coronado Island, Mexico (5-minute Kelp)	2	1–25
Papalote Bay, Mexico	4	8–55
Turtle Bay, Mexico	1	78
Summary: mean = 17, variance = 500.9		

* La Jolla transect site data treated as a single survey with its mean value.
† Gaviota not included. Sheephead were consistently absent in this area. (8 transects conducted)

TABLE 18

Summary of Statistics on Blacksmith Densities From the La Jolla Transect Site, 17 Transects *

Data	Mean	Variance	Standard deviation
Raw			
All counts	392.47	74,403	272.8
Transformed ($\log_{10}(N+1)$)			
All counts	2.450	.1757	.4192
95 percent confidence limits for the mean = ± .216			
Early vs. late			
First 8 transects (N = 8)	2.389	.1891	.4348
Last 8 transects (N = 8)	2.515	.2034	.4510
Reconverted from "all counts" above			
Average 448 fish per acre	--------	--------	--------
Upper confidence limit 739			
Lower confidence limit 272			

* Averages used for paired out and in counts because of their high degree of correlation (see text).

figure for the areas investigated. The data are too variable to warrant further numerical comparisons.

The data on blacksmith, *Chromis punctipinnis,* from the La Jolla transect site showed a high variance in relation to the mean, and the two statistics were brought into a more useful relationship by the $\log_{10}(N + 1)$ transformation (Table 18). Clumped distribution was the rule for this species and large schools typically occur about or above rocky underwater prominences. Out and in portions of transects cover the same terrain and the schools are relatively stationary. Hence it would be expected that the paired out and in estimates of density would show a regression coefficient near 1.0 and a high degree of correlation. These relations held for the La Jolla transect site counts (slope, raw counts, = 0.887, r = 0.788; r significant when greater than 0.515). Because of correlation between out and in counts within pairs, they were averaged for each transect before the data were transformed for further consideration.

TABLE 19

Abundance Classes of Blacksmith (Number per Acre)

Transformed transect data, $\log_{10}(N + 1)$; Gaviota not included because species apparently absent from the area.

$\log_{10}$ class and arithmetic equivalent in parentheses	Site	N transects
0.0–0.9 (0.0–7.8)	Bathtub Rock	2
	Coronado Is., Mexico (5-minute Kelp and South Island)	2
	La Jolla	1
	Papalote Bay, Mexico (2 sites)	3
	Point Loma (3 sites)	4
	Turtle Bay, Mexico	1
1.0–1.9 (7.9–87)	Bird Rock (2 sites)	2
	Guadalupe Is., Mexico (1 site)	1
2.0–2.9 (88–879)	Bathtub Rock	2
	Bird Rock (other than above)	1
	Coronado Is., Mexico, (5-minute Kelp)	1
	Guadalupe Is., Mexico (3 sites, including above)	3
	La Jolla (other than above)	1
	La Jolla transect series (3 in 1.0–1.9 category, 14 in 2.0–2.9 category)	17
	Papalote Bay, Mexico (other than above)	1

Chromis densities averaged considerably higher for the last eight transects at the La Jolla transect site than the first (560 fish per acre vs. 403), but the difference was not significant in the transformed data (t = —.601; rejection region = t —2.14 or 2.14). There may be a biological justification for an increase, because Limbaugh (1955) and Turner and Ebert (1962) both noted that this fish breeds in June. It is possible that aggregation increases progressively prior to this time. The transformed data shows a smaller coefficient of variation (16 percent) than for either the kelp bass or sheephead.

Between-site variation, as well as between-transect variation, was considerable in some areas (Table 19). Principal reasons appear to be the schooling habit of blacksmith and chance inclusion of one or more schools in the transect belts. Rocky-bottom relief appears important to the species. Blacksmith were not encountered during eight transects and associated dives in kelp on a sand bottom at Gaviota. Counts were low at all Point Loma sites. A single transect at Turtle Bay, Mexico, also yielded a low count, although rock of low to moderate relief was present. Considerable densities of blacksmiths were encountered in at least some of the transects at all other sites. Undoubtedly other ecological factors, such as water temperature and turbidity, exposure to food-bearing currents, turbulence, and density of demersal algae and invertebrates, play a definitive role in determining the density of this species. Presence of blacksmiths in moderate to very heavy density along the boulder-strewn underwater slopes of Guadalupe Island (Table 19) demonstrates that giant kelp is not a prerequisite for abundance of this species. Cumulative data on densities indicated a disproportionate number of low estimates in beds of moderate to heavy kelp density and a disproportionate number of high estimates in areas where kelp was light or absent (Table 20).

TABLE 20

Chi-Square Test of Frequency of Blacksmith Densities at Two Levels of Kelp Density

Fish density in terms of the $\log_{10}(N + 1)$ transformation.
Theoretical values in brackets.

Kelp density	Blacksmith per acre	
	≤ 1.3	≥ 1.4
Absent or light	2 (4.85)	7 (4.15)
Moderate to heavy	12 (9.15)	5 (7.85)
	$\chi^2 = 5.55$	

95 percent level = 3.84

Density estimates of these and other fish species encountered at various sites during the transect studies are summarized in Table 21.

Evaluation of the Belt-Transect Estimates

Detailed consideration of the belt-transect data has disclosed numerous possible sources of inaccuracy and bias. The foregoing conclusions regarding population densities must be regarded as tentative until further intensive work is conducted on the various species. One important complication is behavior of fish in respect to divers. Whether a fish ignores, swims toward or swims away from a diver will depend not only upon species response patterns but also on learned behavior prior to the survey. Where repeat surveys are made in the same area, the learning will also include a gradual conditioning to the presence of divers. So, theoretically at least, a true replicate experiment might be impossible for a species that reacts to divers. Other plausible factors of unknown importance that could condition fish behavior include degree of sportfishing in the area, amount of predation (seals, sea lions, large fish), diver activities (abalone hunters probably make food available

TABLE 21

Belt-Transect Estimates of Fish Densities

Estimates for surveys that include two or more transects. Because they were quite variable, calculated densities should be used only for general interpretation. The following are the number of replications and dates: Gaviota (30–55′), 6 transects in July 1960; Gaviota (30′), 2 transects in September 1960; Bathtub Rock, 2 transects, July and September 1959; La Jolla survey site, 17 transects in February through May 1960; Point Loma shelf, 2 transects in December 1959; Guadalupe Island, Mexico, 4 transects in January 1960. Species moderately restricted to broken rock are marked with a single asterisk, and species strongly restricted are marked with two asterisks; much higher density estimates should be possible for these species because few transects, with the exception of Guadalupe Island and Bathtub Rock, contained more than 50-percent broken-rock bottom.

Species Place and depth	Adults per acre (Arithmetic averages)	Remarks
Kelp bass (*Paralabrax clathratus*)		
Gaviota (30–35′)	5	Medium sized; dense kelp; sand and mud; light fishing.
Gaviota (30′)	182	Average for boat channel through bed; juvenile-small adults; dense kelp; sand and mud; light fishing.
Guadalupe Island, Mexico (30–35′)	55	Large sized; no kelp; high-relief rock; none to light fishing.
Papalote Bay, Mexico (35–72′)	10	Medium sized, moderate-dense kelp; sand and moderate-relief rock; light fishing.
San Diego, Bathtub Rock (25′)	46	Small sized; moderate kelp; sand and moderate relief rock; light fishing.
San Diego, La Jolla transect site (65′)	19	Medium sized; no kelp; low-relief rock; moderate fishing.
San Diego, Point Loma shelf (55–70′)	23	Medium sized; moderate kelp; moderate-relief rock; moderate fishing.
Topsmelt (*Atherinops affinis*)		
Gaviota (30–35′)	176	Average for outside edge of bed, in canopy, none encountered in other transects although known to be present; dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	None	No kelp; high relief rock.
Papalote Bay, Mexico (35–72′)	None	Moderate-dense kelp, transects below normal species habitat.
San Diego, Bathtub Rock (25′)	None	Sometimes common in this habitat; moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	None	No kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	56	112 per acre in one transect through canopy; moderate kelp; moderate-relief rock.
Kelp perch (*Brachyistius frenatus*)		
Gaviota (30–55′)	254, 16	Higher values along outside edge of bed; dense kelp; sand and mud.
Gaviota (30′)	382	Along boat channel in bed; dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	None	Present about *Eisenia* and *Sargassum* but none encountered in transect areas; no kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	Abundant	On some transects but not counted. Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	None	New kelp bed and species probably not established as yet; moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	None	No kelp; low relief rock.
San Diego, Point Loma shelf (55–70′)	None	Moderate kelp; moderate-relief rock.
Black perch (*Embiotoca jacksoni*)		
Gaviota (30–35′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	3	No kelp; high-relief rock.

TABLE 21—Continued

Species Place and depth	Adults per acre (Arithmetic averages)	Remarks
Black perch (continued)		
Papalote Bay, Mexico (35–72′)	Present	None encountered on transects. Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	3	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	None	No kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	7	Moderate kelp; moderate-relief rock.
Blacksmith (*Chromis punctipinnis*)*		
Gaviota (30–55′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	349	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	71	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	133	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	57–935	Counts increased during spring; no kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	1	Moderate kelp; moderate-relief rock.
Garibaldi (*Hypsypops rubicunda*)**		
Gaviota (30–55′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	13	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	1	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	16	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	1	No kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	None	Moderate kelp; moderate-relief rock.
Señorita (*Oxyjulis californica*)		
Gaviota (30–55′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	92	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	463	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	72	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	9	No kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	42	Moderate kelp; moderate-relief rock.
California sheephead (*Pimelometopon pulchrum*)		
Gaviota (30–55′)	None	Dense kelp; sand and mud; light fishing.
Gaviota (30′)	None	Dense kelp; sand and mud; light fishing.
Guadalupe Island, Mexico (30–35′)	10	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	26	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	3	Moderate kelp; sand and moderate-relief rock; light fishing.
San Diego, La Jolla transect site (65′)	14	No kelp; low-relief rock; moderate fishing.
San Diego, Point Loma shelf (55–70′)	11	Moderate-kelp; moderate-relief rock; moderate fishing.
Opaleye (*Girella nigricans*)		
Gaviota (30–55′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	8	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	39	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	56	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	trace	No kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	8	Moderate kelp; moderate-relief rock.
Halfmoon (*Medialuna californiensis*)		
Gaviota (30–55′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	5	No kelp; high-relief rock.

TABLE 21—Continued

Species Place and depth	Adults per acre (Arithmetic averages)	Remarks
Halfmoon (continued)		
Papalote Bay, Mexico (35–72′)	None	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	8	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	trace	No kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	2	Moderate kelp; moderate-relief rock.
Kelp rockfish (*Sebastodes atrovirens*)		
Gaviota (30–55′)	1	One transect with 8 per acre along outside edge of bed, others with none; dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	None	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	4	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	None	Moderate kelp; sand and moderate-relief rock
San Diego, La Jolla transect site (65′)	trace	Five seen in 17 transects; no kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	None	Moderate kelp; moderate-relief rock.
Gopher rockfish (*Sebastodes carnatus*)**		
Gaviota (30–55′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	None	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	trace	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	None	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	None	No kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	4	One transect with 9 per acre, the other with none; moderate kelp; moderate-relief rock.
Painted greenling (*Oxylebius pictus*)**		
Gaviota (30–55′)	None	Dense kelp; sand and mud.
Gaviota (30′)	None	Dense kelp; sand and mud.
Guadalupe Island, Mexico (30–35′)	None	No kelp; high-relief rock.
Papalote Bay, Mexico (35–72′)	None	Kelp moderate-dense; sand and moderate-relief rock.
San Diego, Bathtub Rock (25′)	None	Moderate kelp; sand and moderate-relief rock.
San Diego, La Jolla transect site (65′)	trace	Up to 5 per acre in transects that include broken rock; no kelp; low-relief rock.
San Diego, Point Loma shelf (55–70′)	4	Up to 9 per acre in transect that included 50 percent broken rock; moderate kelp; moderate-relief rock.

to fish and thereby attract them; spear-fishermen probably induce wariness), hunger, breeding condition, water termperature, and the degree to which individuals of a species monitor the activities of their neighbors. Inspection of the data discloses numerous unexplained fluctuations in the raw data. Out counts of kelp bass from the La Jolla transect site, for example, average approximately 41 percent larger than the in counts (Table 14) and in the sheephead data the early transects were larger than the late transects by a similar percentage (Table 16). Early blacksmith counts were approximately 38 percent lower than later ones (see text). These differences do not test as significant, but even if they do, would not have altered the conclusions materially. For more sensitive measurements, great care will have to be taken in planning and execution. Ninety-five percent confidence limits for mean counts ($\overline{X}$) of kelp bass, sheephead, and blacksmith at the La Jolla transect site lie well within the region defined by X/2 and 2X. This is considered reasonable accuracy and adequate for the relatively gross comparisons drawn.

Quantitative Collections

All specimens were measured after preservation for estimating fish biomass. Lengths were converted to weights by means of weight-length regressions prepared from museum specimens and freshly collected material. Deducing fresh weights from measurements on preserved fish introduced only negligible errors.

Of the four quantitative collections attempted, three were regarded as successful. The net was not completely closed on the fourth, unsuccessful collection, and an alongshore current carried poison out of the enclosed area before it could affect fish. The discussion will pertain only to the first three collections (two with the wall net, one with ichthyocide and explosives).

The first study was made during June 1958, prior to completion of the wall net. The site chosen was a section of kelp projecting from an offshore bed south of Del Mar, approximately 5 nautical miles north of the Scripps Institution of Oceanography (Figure 23). David H. Davies planned and supervised the operation; 16 SCUBA divers were utilized. Average depth was 35 feet and the area measured approximately 190 x 300 feet (1.31 acres). Both dynamite and Pro-noxfish were used. Twenty-four species of fish were obtained (Table 22).

The second collection was run on July 29, 1959 off Bathtub Rock, an area of young kelp on rocky substrate approximately 3 nautical miles north of the Scripps Institution of Oceanography (Figure 23). The collection utilized Pro-noxfish within the newly constructed wall net. Substrate at the second site was dominated by undercut boulders set in sand. Young *Macrocystis* sporophytes abounded and reached heights of 10 to 12 feet but formed no surface canopy since the depth averaged 25 feet. SCUBA observations from previous years (W. J. North, Conrad Limbaugh, and others, personal communication) indicated the kelp in this bed was regularly removed by winter and spring storms which buried the rocks in sand. Such environmental instability probably explains the nearly complete absence of abalones and sea urchins in the area. Twenty-six fish species were taken from the 0.54 acre that was enclosed (Table 22).

The third collection was on August 10, 1959, in a rocky bay on the south side of Punta Banda, a volcanic peninsula south of Ensenada, Baja California (Figure 23). The net was laid around a section of kelp projecting seaward from an alongshore bed. Kelp plants rose 35 feet from a bottom of flat boulders, cobbles, and sand and terminated in a dense surface canopy. In contrast to Bathtub Rock, there were numerous abalones (mainly red (*Haliotis rufescens*), but also some pink (*H. corrugata*), white (*H. sorenseni*), and one black (*H. cracherodii*) according to Conrad Limbaugh). Many sea cucumbers (*Stichopus* spp.) and giant sea urchins (*Strongylocentrotus franciscanus*) were also noted. The net enclosed approximately 0.57 acre. A gap of 5 to 7 feet at the ends allowed numerous larger fish to escape (kelp bass, sheephead, and opaleye). Thirty-nine fish species were obtained (Table 22).

TABLE 22

Standing Crop of Kelp Bed Fishes, Based on Three Quantitative Collections

Species	Pounds per acre		
	Del Mar	Bathtub Rock	Papalote Bay
Branchiostoma californiense	--	--	trace
Heterodontis francisci	--	--	2.12
Sardinops caerulea	--	--	.17
Engraulis mordax	5.99	--	--
Gymnothorax mordax	--	7.69	--
Citharichthys stigmaeus	--	--	trace
Pleuronichthys coenosus	.08	--	1.59
Paralabrax clathratus	25.25	2.13	3.11
Atherinops affinis	.31	--	trace
Sphyraena argentea	--	315.00	--
Trachurus symmetricus	--	.25	7.98
Xenistius californiensis	--	5.67	--
Anisotremus davidsoni	--	.61	--
Cheilotrema saturnum	--	1.19	--
Genyonemus lineatus	.35	--	--
Caulolatilus princeps	--	--	2.61
Brachyistius frenatus	12.39	--	10.08
Embiotoca jacksoni	11.32	7.98	9.70
Embiotoca lateralis	--	--	2.82
Hyperprosopon argenteum	.14	--	--
Hypsurus caryi	1.68	--	.65
Phanerodon furcatus	5.08	trace	--
Rhacochilus toxotes	4.24	--	3.35
Rhacochilus vacca	14.62	.28	7.65
Chromis punctipinnis	.03	.15	1.84
Hypsypops rubicunda	--	29.83	--
Halichoeres semicinctus	--	.70	--
Oxyjulis californica	20.33	.66	.09
Pimelometopon pulchrum	--	--	2.63
Girella nigricans	41.36	13.30	6.70
Medialuna californiensis	3.75	.86	--
Scorpaena guttata	.68	4.34	1.19
Sebastodes atrovirens	29.00	--	12.52
Sebastodes auriculatus	--	1.31	--
Sebastodes carnatus and *chrysomelas*	--	1.03	--
Sebastodes paucispinis	--	--	trace
Sebastodes rastrelliger	1.85	1.31	--
Sebastodes serranoides	--	--	--
Oxylebius pictus	--	--	1.50
Artedius corallinus	--	--	.12
Artedius creaseri	--	trace	trace
Leiocottus hirundo	.06	--	.99
Orthonopias triacis	--	--	.29
Liparis mucosus	--	--	.13
Syngnathus californiensis	.12	--	.05
Lethops connectens	trace	--	--
Porichthys myriaster	--	4.10	--
Gobiesox rhessodon	--	trace	trace
Gobiesox new sp.	--	--	trace
Paraclinus integripinnis	--	.07	--
Heterostichus rostratus	3.20	5.58	13.54
Alloclinus holderi	--	--	.97
Gibbonsia elegans	--	2.46	2.85
Gibbonsia metzi	--	--	1.26
Gibbonsia montereyensis	--	--	.05
Neoclinus stephensae	--	--	.07
Hypsoblennius sp.	--	.07	--
Undescribed genus, sp. #1	--	--	.03
Undescribed genus, sp. #2	--	--	trace
Ulvicola sanctaerosae	--	--	trace
Otophidium taylori	.32	--	.66
Totals	182	406	99
Other			
Lobster	None	97	None
Octopus	None	5	5

Combined Estimates

A serious limitation on the use of the belt transect for biomass estimation lies in the error inherent in conversion of estimates of fish size to fish weight. It is reasonable to expect at least 20 percent average diver error in fish-length estimates. Since the normal relationship of weight to length is approximately cubic (Appendix B) any error is magnified when lengths are converted to weights. Overestimation of length is commonest, since the faceplate magnifies objects by approximately 25 percent.

The most reliable estimate available of average size for kelp bass in the San Diego area is the length-weight data that were obtained from concurrent studies in the sportfishery (See Chapter 7). Although undoubtedly somewhat biased, the sportfishery average of 953 grams or approximately 2.1 pounds per adult fish seems reasonable, judging from other experience with the species.

Calculations for average size of sheephead are more tenuous than for kelp bass because length and weight frequency distributions from the sportfishery were severely biased toward large fish. The quantitative collections did not yield enough sheephead to give a reliable estimate. As a result, the average weight of adults in the study regions was arbitrarily considered 2.5 pounds, a value that seems reasonable but possibly may be somewhat low, because individuals weigh up to 30 lbs. (Roedel, 1953).

Chance encounters with schools of adult opaleyes caused great variation in wall-net and belt-transect estimates; hence these data were also analyzed for average densities (Table 23). Highest densities occurred in the shallower section of the rocky-inshore region, although both single individuals and schools were found to depths of 65 feet and more. Higher densities were correlated with *Macrocystis* but direct causal

TABLE 23

Transect Estimates of Opaleye Density

Out and in halves of transects averaged. Means marked with an asterisk were reconverted from log $_{10}$ (N+1) normalized data, after Barnes (1952).

Habitat	N transects	Adults per acre	
		Range	Average
Shallow (0–35 feet)			
Kelp none to light	6	0–65	16.0
Kelp moderate to heavy			
Demersal	5	0–157	65.2
Canopy over deeper water	6	0–20	6.3
Average for kelp moderate to heavy*	11	----	66.5
confidence limits:	16.3 and 256		
Average for shallow*	17	----	40.0
confidence limits:	15.4 and 101		
Deep (42–65+ feet)			
Kelp none to light	19	0–2	0.4
Kelp moderate to heavy	10	0–30	4.5
Average for deep*	29	----	1.3
confidence limits:	0.7 and 2.2		
Average for deep* + canopy average*	--	----	9.3

factors were not established. Increases with depth and with kelp association may both be related to a third factor. Although opaleyes frequently consume large amounts of *Macrocystis* when available, they also feed heavily on moss-like red algae of the shallow inshore zone. An average weight of 1.8 pounds was computed from the Del Mar collection, in which opaleye were fairly well represented.

The first set of the net indicated that kelp bass, sheephead, and opaleye would be underestimated by the quantitative collection method. Large fish noted within the enclosure at the beginning of the poison operation did not materialize in the pickup and could not be located in the immediate area. In all three collections density values for large species are well below transect estimates in the same area and also below subjective impressions of density estimated from other dives at the sites. For these reasons the standing crop estimates from the quantitative collections were revised upward. Transect values for density were multiplied by the factors discussed above for average weight of adults of the three species (Table 24). Averages for estimates of resident fish for the three collections varied from 296 to 335 pounds per acre and averaged 313 pounds per acre for animal standing crop of some localities (Table 22). Addition of all other inverterbrates could multiply the sum manyfold.

TABLE 24

Corrected Standing Crop Estimates for Fishes

Based on the three quantitative collections with substitution of transect values for kelp bass, sheephead, and opaleye. Applies principally to beds 25–35 feet in depth.

	Pounds per acre		
	Del Mar	Bathtub Rock	Papalote Bay
Transect-based estimates			
Kelp bass[1]	105	105	105
Sheephead[2]	43	43	43
Opaleye[3]	72	72	72
Total	220	220	220
Quantitative collections			
Other fish species	115	391 (76)[4]	87
Total	335	611 (296)[4]	307
Average (excluding barracuda) = 313 lbs. per acre			

[1] Based on average weight of 2.1 lbs. and av. density of 50 per acre (see text and Table 15).
[2] Based on average weight of 2.5 lbs. and av. density of 17 per acre (see text and Table 17).
[3] Based on average weight of 1.8 lbs. and av. density of 40 per acre (see text and Table 23).
[4] Value in parens. excludes barracuda.

A comparison of these estimates with literature values for lakes and coral reefs demonstrated that the kelp bed estimates were close to the median values for the other habitats (Table 25). The present kelp-bed estimates, of course, apply only to resident species that spend their adult lives in association with restricted geographic regions of the rocky-inshore habitat. They do not include neritic species such as anchovy, sardine, barracuda, jack mackerel, bonito and yellowtail.

TABLE 25

Estimates of Standing Crop of Fishes in Kelp Beds of Southern California Compared with Those for Coral Reefs of Hawaii and Bermuda, and U.S. Freshwater Lakes

Data, in part, from Carlander (1950), Brock (1954), and Bardach (1959). Median frequency class underlined.

Pounds per acre	Frequency		
	Lakes	Coral reefs	Kelp beds
5–9	1	--	--
10–19	7	--	--
20–39	13	1	--
40–74	15	--	--
75–149	96	3	--
150–299	48	3	1
300–599	96	2	2
600–1,199	24	--	--
1,200–2,800	2	1	--

Chance sampling of some of these species could increase our standing crop figures by several times.

Nearly all species of the kelp bed biocoenose usually decline with attrition of *Macrocystis*. The causal chain of this collapse is not obvious. The short algæ normally harbor numerous small Crustacea that are important food items (as discussed in Chapter 8); their disappearance means the loss of an important food source for the fishes. During the 1950's the author saw profound changes over much of the rocky inshore region of the Palos Verdes peninsula, near Los Angeles. Heavy kelp-bed areas, rich in fishes and short algae, are now barren rock. Many of these barren areas now display very small standing crops of resident fishes and invertebrates.

SUMMARY

1. Techniques for estimating fish densities included a 558-foot enclosure net and SCUBA surveys of adults along a belt transect.

2. The enclosure-net (wall net) and belt-transect methods were nearly complementary. The net gave the best data on small and cryptic fishes; the transect the best data on large, more motile fishes.

3. Fifteen repeat transects in the same area (La Jolla transect site) over a 3-month period showed no significant differences for kelp bass between the out and in halves of transects or between transects performed in the first and last halves of the series. Populations averaged 20.0 fish per acre with 95 percent confidence limits at 14.5 and 27.4.

4. Although the 15 repeat transects for kelp bass at one site showed no correlation between counts on out and in halves of the transects, there was a high correlation between halves when different sites were compared; i.e., within-site variation was slight in comparison with between-site variation.

5. Population densities of kelp bass were not significantly different between areas of zero to light kelp density and those supporting mod-

erate to heavy kelp density, except where fishing pressure was high. Regions of low kelp density and high fishing pressure had few fish.

6. The giant kelp, *Macrocystis,* is not necessary for the maintenance of dense kelp-bass populations composed of large fish.

7. Although not necessary for the maintenance of kelp bass, indirect evidence suggested that the species prefers some stands of *Macrocystis* to regions where *Macrocystis* is absent.

8. For sheephead as well as for kelp bass, counts for the repeat transect site were not significantly different between the out and in halves of transects or between the first and last halves of the series. Populations averaged 14 fish per acre with 95 percent confidence limits at 12 and 17.

9. For sheephead as well as for kelp bass, within-site correlation between out and in halves of transects was negligible in comparison with correlation when sites were contrasted; i.e., within-site variation was slight compared to between-site variation.

10. The sheephead data show no important differences in respect to effects of kelp density or fishing pressure.

11. Data on blacksmith from the area of repeat transects show high correlation between counts obtained on the in and out halves of transects. This was expected, because the fish are schooling and schools are usually restricted to regions of rocky prominences or broken bottom.

12. In the repeat transect area, blacksmith densities averaged 448 fish per acre, with 95 percent confidence limits at 272 and 739. No significant shift in counts was noted during the 3-month period of survey.

13. Presence of giant kelp is not a habitat requirement for populations of blacksmith. Some data suggest that dense kelp may actually exclude this species.

APPENDIX A

Approximate Cost of Materials Used in the Wall-Net

Materials	Approximate cost (dollars)
Wall-Net	
1,350 ft. ¾'' stretch M-2 Marlon netting, 600-mesh width	1,695
600 ft. 5/16'' diameter, medium grade (not hard) Nylon rope	31
780 ft. 3/16'' galvanized (dipped) iron chain	119
530 #245 Dale plastic floats (yellow)	56
14 lbs. 7-mesh, 1'' stretch synthetic M-6 selvage (tan)	62
1 lb. #24 Nylon twine	2
3 lbs. #36 Marlon twine	11
5 6 lb. anchors	57
Labor	300
Total	2,333
Pumping Equipment	
1 Marine Products Pump #L 9375-A (Centrifugal)	53
1 Continental 1½ HP Motor AV7	43
50 ft. ¾'' (I.D.) garden hose	15
Total	111
Miscellaneous	
3 U.S. Air Force (surplus) oxygen tanks for use as buoys, ea.	2
5-gallon cans Pronoxfish, ea.	25

14. Ninety-five percent confidence intervals for mean counts ($\overline{X}$) of kelp bass, sheephead, and blacksmith in repeat transects at the La Jolla transect site were well within the limits of $\overline{X}/2$ and $2\overline{X}$. This relatively narrow range of variability justified the relatively gross comparisons based on the belt-transect surveys.

15. Opaleye occurred in greater densities in water shallower than 35 feet and in regions of moderate to heavy *Macrocystis* as compared with regions where *Macrocystis* was absent or sparse.

16. Fish biomass in the kelp beds was estimated from three quantitative collections, supplemented by data from approximately 50 belt transects.

17. Three standing crop estimates of resident kelp-bed fishes amounted to 335, 296, and 307 pounds per acre, with 313 as the mean.

18. Incorporating invertebrate biomasses or chance inclusion of schooling pelagic-neritic fish species would multiply values for resident fishes manyfold.

19. Standing crop estimates of resident fishes in kelp beds are close to median values from the literature for lakes and coral reefs.

APPENDIX B

Weight-Length Relationships of Some Common Kelp-Bed Fishes

Based on the equation $\text{Log } y = \text{Log } a + b \text{ Log } x$, which is the logarithmic transformation of $y = ax^b$, where y = weight in grams and x = standard length in mm. An asterisk indicates that the regression was fitted by least-squares; other regressions fitted by eye.

Species (No. specimens)	Size range (mm.)	b	Log a (—)
Gymnothorax mordax (20)	172–781	3.42744	6.95017
Engraulis mordax (20)	46–99	3.86445	6.69548
Pleuronichthys coenosus (8)	61–179	3.19554	5.01939
Paralabrax clathratus >250 mm. (9)	400–500	2.72559	3.90984
Paralabrax clathratus <250 mm. (150)*	87–250	3.25655	5.17812
Atherinops affinis (22)*	83–192	3.03574	5.05253
Xenistius californiensis (7)	105–175	2.89821	4.44896
Genyonemus lineatus (9)	85–161	2.92555	4.58081
Brachyistius frenatus >65 mm. (27)	65–124	3.16859	4.92666
Brachyistius frenatus <65 mm. (16)	42–65	4.51176	7.34690
Embiotoca jacksoni (27)	65–190	3.31179	5.08268
Hyperprosopon argenteum (22)	50–150	3.21745	4.96804
Hypsurus caryi (9)	107–174	3.55784	5.69534
Phanerodon furcatus (19)	97–194	3.11909	4.85490
Rhacochilus toxotes (10)	75–275	3.35526	5.34290
Rhacochilus vacca >80 mm. (7)	80–291	3.03269	4.57282
Rhacochilus vacca <80 mm. (19)	55–80	4.17962	6.75553
Chromis punctipinnis (20)	64–155	3.08997	4.73282
Hypsypops rubicunda (22)	105–220	3.10332	4.44321
Pimelometapon pulchrum (14)	83–283	3.15736	4.88164
Oxyjulis californica (20)	69–150	3.50286	5.89015
Girella nigricans (11)	195–300	2.92881	4.27729
Medialuna californiensis (10)	42–240	3.25843	5.08113
Scorpaena guttata (19)	62–175	2.98126	4.39595
Sebastodes atrovirens (36)	85–285	2.92402	4.37392
Sebastodes carnatus and *chrysomelas* (22)	39–230	3.20956	4.89394
Sebastodes rastrelliger (17)	59–225	3.21492	4.94575
Sebastodes serriceps (17)	45–260	3.08684	4.73930
Sebastodes serranoides (22)	60–230	3.18334	5.10736
Oxylebius pictus† (23)	113–145	2.92764	4.49355
Syngnathus californiensis (17)	185–360	3.95516	8.78641
Gibbonsia elegans (66)	45–115	3.35807	5.55159
Gibbonsia metzi (12)	48–147	3.21058	5.33842
Heterostichus rostratus (40)	57–235	3.32963	5.74121
Otophidium taylori (11)	95–265	3.69585	7.00510

† Probably represents one year-class only.

Erratum: Page 74, line 17 up, for "Gobiesox new sp." read "Gobiesox engrammus."

References for this paper follow reprint no. 131 in this volume.

7. OBSERVATIONS ON THE FOOD AND BIOLOGY OF THE KELP BASS, *PARALABRAX CLATHRATUS* WITH NOTES ON ITS SPORTFISHERY AT SAN DIEGO, CALIFORNIA

JAY C. QUAST
U.S. Bureau of Commercial Fisheries
Auke Bay, Alaska

INTRODUCTION

The kelp bass is widespread and abundant in southern California, and is highly valued by sportfishermen and skindivers. Although usually not preferred to albacore, yellowtail, or barracuda (Collyer and Young, 1953, personal observations), the species is an important staple to the sportfishery because it is abundant, delectable, a good fighter, and available throughout the year. Kelp beds are increasingly used by recreational and commercial interests. The decline of many beds in extent and density during 1957–58 aroused interest in management of the beds and associated fishes. This concern stimulated considerable research on the kelp bass, including a preliminary study by Collyer and Young (1953), life-history notes by Limbaugh (1955), a study of the sportfishery statistics by Davies (1958), and a study of the kelp bass and its fishery by Young (1963). The present work complements that of Young.

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Large samples of kelp bass were made available through the cooperation of several San Diego sportfishing companies and their boat skippers. I am grateful to H and M Sportfishers for permission to accompany the *Mascot III* on trips to the kelp areas, and for permission to use the catch data for analysis. Special gratitude is due to the skipper, Manuel P. Sylva, for assistance during the trips and for his observations on the fishery. *Mascot III* catch statistics were made available by Edward C. Greenhood, Biostatistical Section, California Department of Fish and Game, Terminal Island. Numerous specimens were also obtained through the cooperation of Chili Troester and John Taylor, skippers of the *Seabiscuit* and *Jet*, respectively, Mission Bay Sportfishing Company.

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MATERIALS AND METHODS

Observations were gathered during approximately 200 SCUBA dives in the inshore and island waters of southern and Baja California from 1958 to 1960. Food and gonad condition were determined on more than 1700 specimens, obtained principally while sampling about sportfishing boats and by spearfishing. Population estimates were based on wall-net and belt-transect data, discussed in Chapter 6.

ECOLOGY

The kelp bass is a medium-sized generalized carnivore occupying a relatively wide variety of environmental situations. Some physical relief in the form of rocks, debris, or plant materials characterized the usual habitat. The attractiveness of the environment increases as it becomes more broken or encrusted or overgrown with large laminarian algae. Environmental situations attractive to kelp bass include sparse *Zostera* beds on sandy bottoms, cobble regions, areas of broken rock, submarine canyons, cliffs, and *Macrocystis* beds with bottoms varying from substrates of mud and sand to highly broken rock.

Adult kelp bass occur over a wide bathymetric range, from the surf zone to depths of 130 feet or more. Large adults near La Jolla are common about the submarine canyons which begin at 100 feet and extend downward. They are commonly taken by hook-and-line from depths of 90 to 100 feet by passengers aboard sportfishing boats. Although juveniles and small adults are usually abundant in the surf zone, they are rare in intertidal collections (only one individual occurred in 36 collections by the Scripps Institution of Oceanography and the University of California at Los Angeles). No size-segregation with depth was obvious in kelp beds: adults and juveniles both occurred near the bottom as well as among surface fronds. The deeper bathymetric limits are not definitely known, but kelp bass are rarely reported by divers below 150 feet, and are rare in hook-and-line catches at that depth. A 240-mm adult was taken at 188 feet at Guadalupe Island, Mexico, in January 1960 (Carl L. Hubbs and Allan J. Stover, Jr., personal communication).

Roedel (1953) gave the geographic range of the kelp bass as Monterey Bay, central California, to Abreojos Point (south of 27°N), Baja California, but states that individuals are rare north of Point Conception. The late Conrad Limbaugh noted (personal communication) that individuals were common about all offshore islands of southern California, including the northernmost, San Miguel. He also observed individuals at Alijos Rocks (24° 57′ N, 115° 45′ E), far off southern Baja California. I have found this species in abundance on Guadalupe Island, off the Pacific coast of Baja California, and about the rocks and kelp of the San Benitos Islands and Punta Eugenia (approximately 28° N), near the southern limits of the recorded range.

Population Density

Estimates of the population density of this species for various regions, habitats, and intensity of fishing are presented in Chapter 6. The kelp bass is the most obvious fish inhabitant of the kelp beds and rocky areas, and was noted the most consistently during dives. However, usually it is not the most abundant species in these habitats. Individuals tend to aggregate about broken areas, but definite schools were encountered only rarely. One such concentration included approximately 70 large adults at Guadalupe Island, Mexico, in February 1960. Limbaugh (1955) noted a large spawning aggregation in the kelp beds at La Jolla.

Data from the sportfishery, discussed below, suggest that adults are not restricted to specific territories but shift in response to site preference and lowered population density at the preferred sites. Densities from near-average to higher-than-average were encountered at certain sites frequented by the sportfishing boats, even at the end of a fishing season. One such site gave an estimate of 16 adults per acre after the end of a fishing season, although at least 200 adults had been taken weekly from the site during several preceding 2-month periods by the *Mascot III*.

BEHAVIOR

The kelp bass is strongly curious, and usually will be encountered in the vicinity of some kind of cover. In the La Jolla region, where spearfishing is frequent, the distance maintained from a diver by a kelp bass is usually directly proportional to the bass size: large juveniles typically approach to within a yard, adults will usually stay a yard or more away, and large adults in general remain more than 12 feet distant. In several regions about La Jolla such as the mouths of the submarine canyons (not frequented by spearfishermen), large adults may easily be obtained with an 8-foot pole spear. Small adults will often accompany a diver, swimming several feet to his side or behind. When the diver turns to face the fish they usually move to a greater distance. In the upper water layers about the kelp canopy, the bass seem more reluctant to leave the vicinity of cover to inspect the diver and usually remain within a few feet of the kelp columns, obviously keeping the diver under observation. In all regions juveniles and young adults stay within a shorter radius of cover than adults. When approached in the canopy, the younger fishes move down the kelp column. I have ''herded'' young bass through a strong thermocline in such manner. Numerous other observations indicate that kelp bass rely on the kelp for cover. Small adults wounded by a spear sometimes dart into a column of kelp stipes and fronds and align themselves, motionless, with the stipes. Larger adults may sometimes be approached more closely when they are among kelp fronds, even when the diver is under surveillance, because the fish apparently feel more secure near cover.

Kelp bass and other kelp-bed fishes can detect alignment of elongate objects, and often take evasive action when spears are pointed at them. Individual kelp bass, however, sometimes approach the five-tine spear head closely when it is not pointed at them. To see if the alignment cue was visual, a pole spear was fashioned with a 4-foot Lucite tip (Lucite has nearly the same optical and acoustical properties as water). The Lucite, however, was plainly visible to the divers underwater and kelp bass took the same evasive action. Movement and alignment are probably readily perceived by this species and probably play important roles in food-getting and defense. Narrowly missed or even lightly wounded juveniles and small adults return for several seconds to the immediate scene of the miss, with fins erect, before swimming away rapidly.

In agreement with Limbaugh's (1955) findings, aggressive actions between kelp bass were not noted in the field. A juvenile held in a 15-gallon glass aquarium with juvenile black croaker of similar size, however, displayed numerous degrees of aggressiveness. In order of apparent increasing aggressiveness the following actions were directed against the croaker: raising the dorsal spines when the other fish approached; stiffening the body, aligned head to tail with the other fish, with slight tail-slapping movements; actual combat, with very rapid action that was difficult to interpret. Approach by the croaker to a small cave normally used by the bass and live food in the aquarium evoked especially strong aggressive action by the bass. The only injury noted from the nearly daily combat between the fishes during 7 months was one corneal tear in the croaker, which healed within 1 week. The combat was witnessed and the damage was apparently inflicted by the bass's opercular or preopercular spine.

Digging actions by the aquarium-held specimen were noted, but were rare. The fish backed into a crevice between the rocks and moved sand forward with the pectoral fins. Several crevices between the sand and rock were used as hiding places when the aquarium was severely disturbed. Similar hiding behavior by injured fish was observed in the field.

Visibility probably determines the distance that kelp-bed fishes wander from cover. Adult bass were not seen beyond visibility range of permanent or semi-permanent landmarks such as the bottom, kelp columns, or kelp canopy. In very turbid water, bass were encountered only very close to cover, usually adjacent to rocks or in crevices between or under rocks. When the water was very turbid near the bottom however, bass and other kelp-bed fishes were frequently encountered well off the bottom, and about the kelp in the clearer waters above.

FISH MOVEMENT AND HOME RANGE

On the basis of a tagging and length-frequency study, involving nearly 4,000 marked fish, Collyer and Young (1953) concluded that the data ''strongly suggest that the kelp bass fishery is based on a series of independent populations.'' Over 400 fish showed ''no movement,'' 23 fish moved from a few hundred yards to 4 miles, and 16 kelp bass strayed a distance of 5 miles or more. In a related study near La Jolla, Limbaugh (1955) trapped, tagged, and released kelp bass in cut and uncut sections of a kelp bed to determine fish movements and possible preferences for harvested or unharvested kelp. Some fish moved for varying distances (Figure 24), but no preference for cut or uncut sections could be determined from the data. Recaptures approached the zero asymptote at around six units of about 470 feet, hence five units (slightly more then one-half mile) is a reasonable estimate for maximum range. If this distance is taken as the diameter of a circle, the actual area involved is approximately 125 acres. However, the bearing of these data on the home range of this species in offshore kelp beds is open to question because the prime bass habitat in the area investigated by Limbaugh was limited in part to a narrow rocky subtidal zone. The fish undoubtedly have differently shaped home ranges within offshore beds, possibly of less area than that calculated from Limbaugh's data.

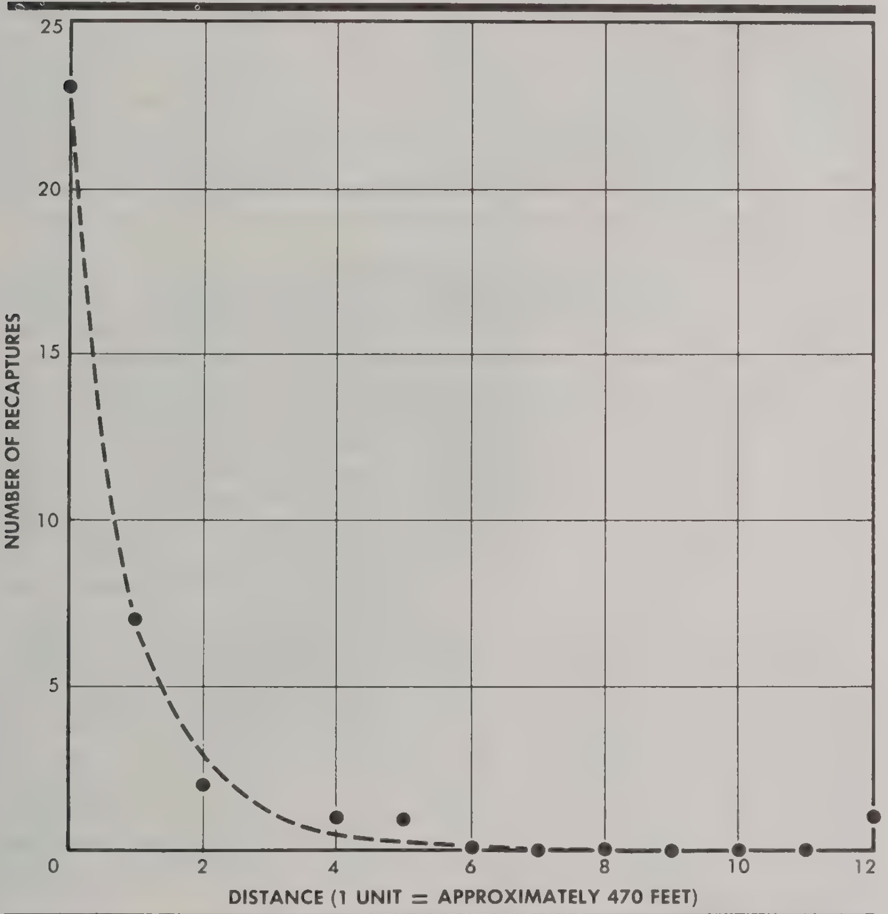


FIGURE 24. Distance-of-recapture frequencies for tagged kelp bass. Data from Limbaugh (1955).

FOOD

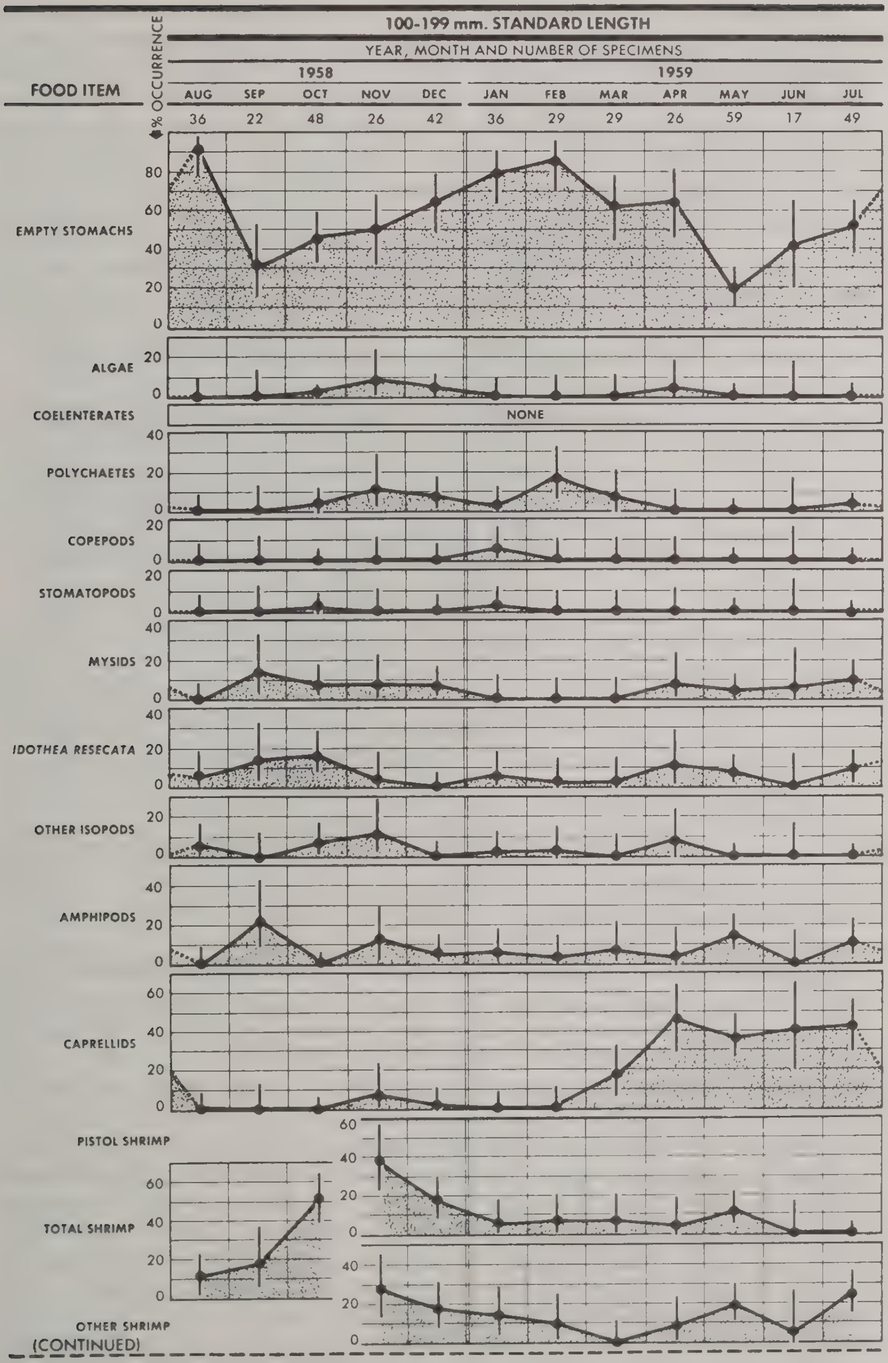
The majority of the approximately 1700 digestive-tract samples collected between August, 1958 and July, 1959 were obtained from sportfishing boats: less than 25 percent were collected with spear and SCUBA. Approximately two-thirds of the sportfishing boat samples were from kelp beds at Point Loma, San Diego. Nearly all SCUBA samples were from kelp beds at La Jolla, 10 nautical miles northward.

A principal purpose of the SCUBA sampling was to expose any extreme bias in the sportfishing data, in addition to the known bias toward the northern anchovy, *Engraulis mordax,* used almost exclusively as live bait during the sampling period. The SCUBA samples were more variable than expected and sufficient kelp bass could not be obtained to permit reliable comparisons with sportfishing boats. Differences between the areas made valid comparisons difficult. The La Jolla and Point Loma beds are well separated and the two localities differ significantly in bottom character, wave exposure, and water quality (The Point Loma bed was frequently exposed to the relatively polluted waters of San Diego Bay). Sportfishing boats also operate near the La Jolla beds and release large quantities of live anchovies, some of which had undoubtedly been taken by the spear-collected specimens, complicating analysis. Because the SCUBA-obtained samples could not be evaluated satisfactorily, and because the samples generally resembled those from the sportfishing boats, the data from the two sources are lumped.

Food items from the digestive tracts were analyzed for frequency of occurrence by monthly samples, or by longer periods for small samples (Figures 25 to 27). Volumes were not used because large volumes for anchovy bait were common. Also remaining items, especially from the intestines, were frequently very well-digested. Stomachs only were examined during the first 2 months. Intestinal contents, however, were found valuable to the study and doubled or trebled the food data per fish. Intestinal items usually could be identified to class or family, and crustaceans frequently remained partly intact or had parts that could be identified even when they were nearly through the digestive tract. Axial skeletons of fishes frequently were sufficiently intact to be identified to family and some to species. Empty stomachs were frequent, even in the sportfishing catch, although the change in pressure on fishes brought from the bottom normally was not enough to evert their stomachs (average change was estimated as approximately 70 feet, equivalent to two atmospheres). Most frequent prey species are listed separately, but other items are grouped under higher taxa. For example, isopods were split into *''Idothea resecata''* and ''other isopods'', and shrimp into ''pistol shrimp'' (*Alphaeus spp.*) and ''other shrimp''. Five levels of utilization were based on frequency of occurrence: trace, indicated two percent or less; low, 3 to 24 percent; moderate, 25 to 46 percent; heavy, 47 to 68 percent; and very heavy, more than 68 percent.

100–199 mm Fish (Figure 25)

The data for fish of this size range indicate that crabs and ''other shrimps'' are very important. The crab entries between August 1958 and January 1959 represent principally small spider crabs (approximately 1 cm or less from rostrum tip to posterior edge of carapace), which abound in the short algae of the bottom. Crab entries after January are almost entirely for red crabs, *Pleuroncodes planipes,* which were exceptionally abundant in coastal southern California and Baja California during that spring. Entries for ''other shrimps'' represented numerous small, poorly known, demersal species. Kelp isopods (*Idothea resecata*), amphipods, and pistol shrimp appear consistently. Kelp isopods are frequently seen in abundance in the kelp canopy. The large adults, about 2.5 cm long, may be seen clinging to the fronds and stipes or swimming from stipe to stipe (when swimming, isopods hold the two large antennae together in front, possibly for streamlining). Little is known concerning the vertical abundance or


100-199 mm. STANDARD LENGTH
YEAR, MONTH AND NUMBER OF SPECIMENS
1958
1959
FOOD ITEM
% OCCURRENCE
AUG 36
SEP 22
OCT 48
NOV 26
DEC 42
JAN 36
FEB 29
MAR 29
APR 26
MAY 59
JUN 17
JUL 49
EMPTY STOMACHS
ALGAE
COELENTERATES
NONE
POLYCHAETES
COPEPODS
STOMATOPODS
MYSIDS
IDOTHEA RESECATA
OTHER ISOPODS
AMPHIPODS
CAPRELLIDS
PISTOL SHRIMP
TOTAL SHRIMP
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0
20
40
60
80
(CONTINUED)

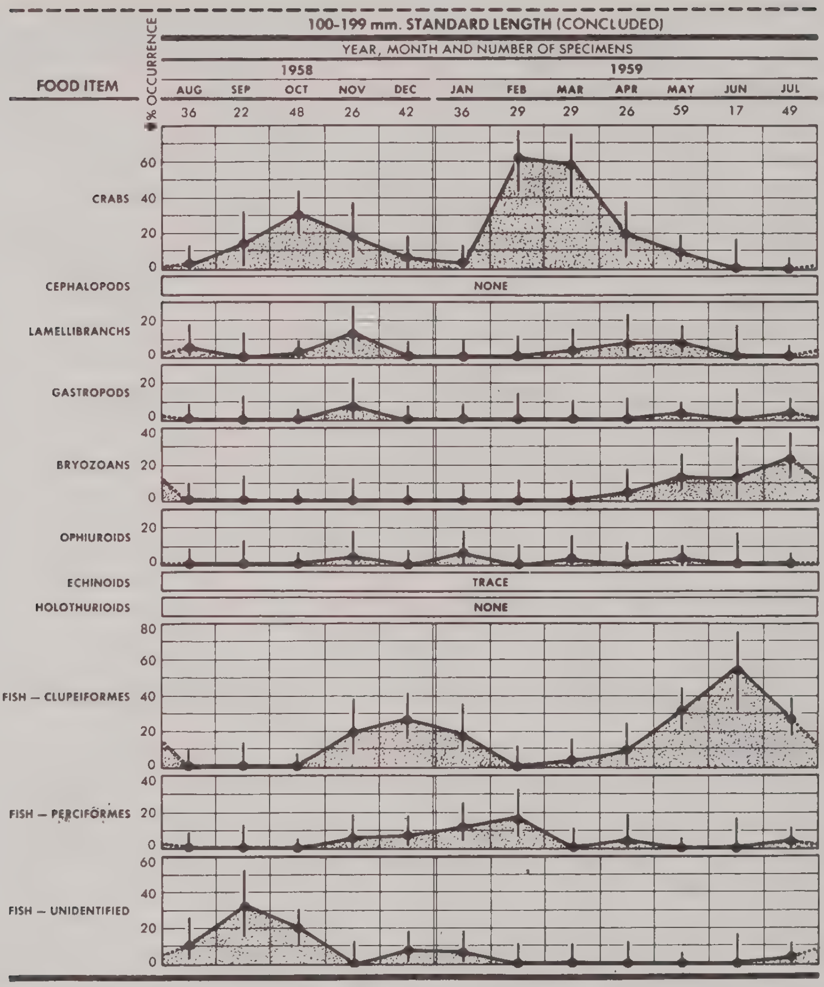


FIGURE 25. Food of 100–199-mm kelp bass. Data from specimens collected by hook-and-line and spear, from the San Diego region except for February, 1959, for which specimens were from the San Benito Islands (lat. 28° N.).

life history of this important forage species. Gammarid amphipods abound in the kelp-bed environment and many species were noted in the digestive tracts. Both spider crabs and gammarid amphipods abound in the short algal growths of rocky bottoms and gammarid amphipods also occur on all parts of the kelp plants. Pistol shrimp inhabit burrows and crevices and are common about some kelp beds. Sometimes their steady noise, reminiscent of crackling cellophane, is audible through a skiff bottom. Although several species occur in kelp beds, adults of *Alphaeus dentipes* constitute the principal dietary contribution. Mysids and caprellids also are important. Caprellids and an associated tufted bryozoan, *Bugula neritina,* peak in the indicated diets during late spring and early summer. The caprellids then abound in the kelp canopy. The bryozoans probably were ingested incidentally with the caprellids.

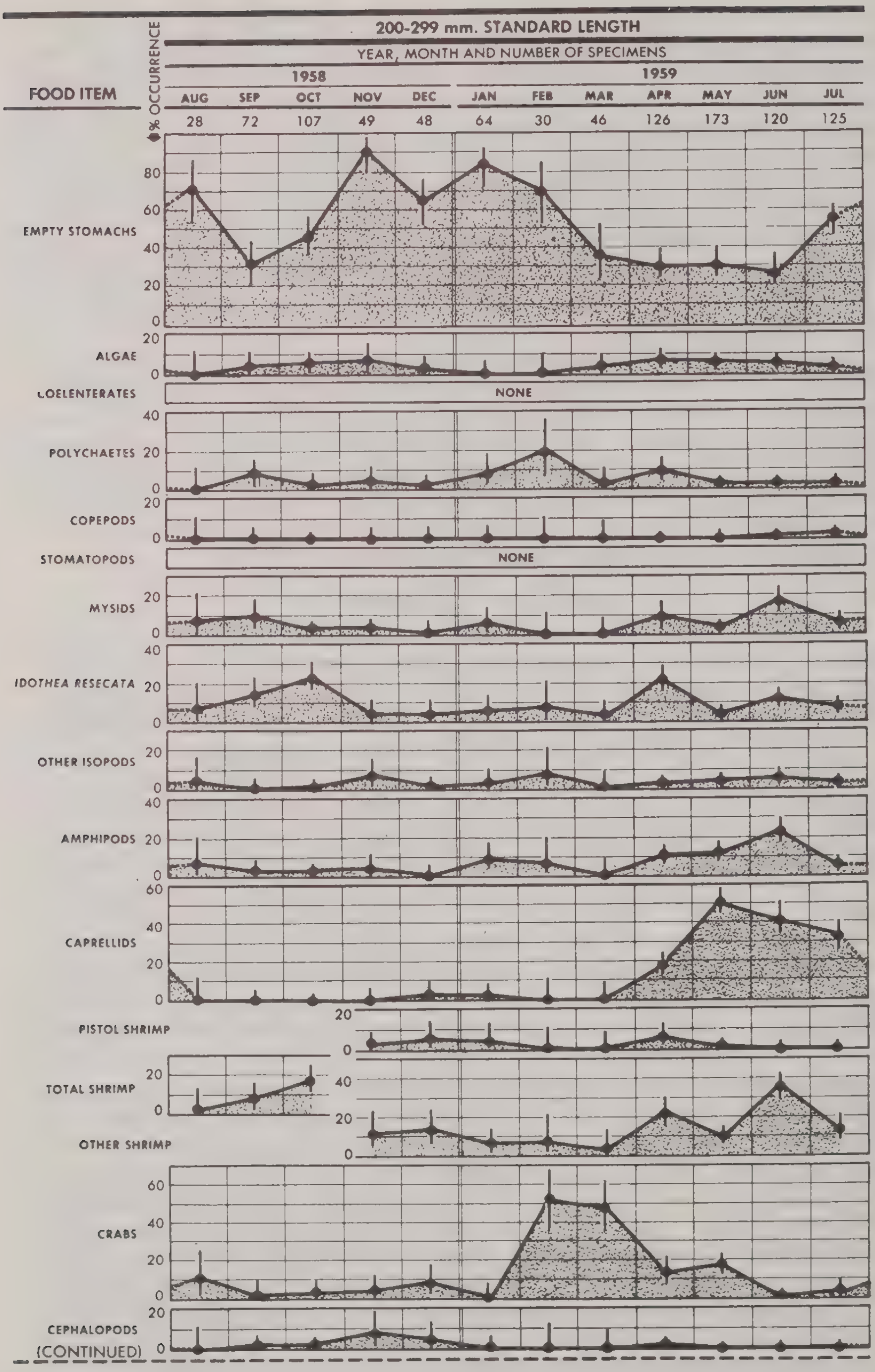
Fish constitute an important item on the food list and the northern anchovy, a clupeiform fish, is undoubtedly highly preferred. Live anchovies are the bait of choice for sportfishing boats in kelp beds and sometimes bass repeatedly break the water surface pursuing live bait when a sportfishing boat circles and establishes a ''chum line'' before anchoring. Anchovies were abundant adjacent to and within kelp beds during the year of study so presumably they also contributed importantly to the fish's natural diet. Perciform (spiny-rayed) fishes also were important, but most entries were unidentifiable to species. Among those identified were a flatfish, an eel-blenny, one goby, one kelp bass, five giant kelpfish, and three cottids (one *Artedius* sp.), all of relatively small size.

Summation of all categories revealed two general feeding peaks, one during fall and one during spring. Normally, ocean surface temperatures off La Jolla rise during April and May and lower abruptly sometime during November or December at the onset of winter storms. Nearly all food categories were represented in the fall feeding peak, possibly because a wide range of organisms was made available by the storms. The spring feeding peak was more restricted, and was characterized by an increase in caprellids, crabs and fish.

200–299 mm Fish (Figure 26)

Frequencies resemble those of the first group above with the inhabitants of the kelp canopy possibly increasing slightly in importance. Kelp isopods occur most consistently but are never abundant, and polychaetes, gammarid amphipods, ''other shrimps'', and crabs are nearly as consistent. A nereid similar to a 5-cm species common in the canopy, predominated among polychaetes. Gammarid amphipods included the relatively large kelp curler, *Ampithoe humeralis,* also common in the canopy, as well as many smaller forms that are possibly from the kelp canopy as well. Sources of ''other shrimps'' are unknown. Habits of the various shrimp species have not been studied, but at least one, the ''abalone'' shrimp (*Baeteus harfordi*) includes the kelp canopy in its habitat. In contrast to the smaller size-class of kelp bass discussed above, demersal spider crabs were not important in the fall feeding peak. As for the smaller fish a spring crab peak was from the often-pelagic red crab, *Pleuroncodes planipes,* and entries for the demersal species remained infrequent. Fish again were very important with Clupeiformes in moderate to high occurrence, presumably because the samples were taken aboard sportfishing boats. Spiny-rayed fishes occurred at low levels, but undoubtedly are important because some items were relatively large in size. Included were giant kelpfish (with a frequency nearly as great as for all other identified spiny-rayed fishes), flatfishes, pholids, labrids, cottids, embiotocids, gobies, and kelp bass.

Two general feeding peaks are again apparent. The fall peak had a broad spectrum of food types, with the majority at low frequency, as well as moderate feeding on clupeiform fishes. The spring peak showed intensive feeding on caprellids and clupeiform fishes. Empty stomachs were less frequent during feeding peaks.


200-299 mm. STANDARD LENGTH
YEAR, MONTH AND NUMBER OF SPECIMENS
1958
1959
FOOD ITEM
% OCCURRENCE
AUG 28
SEP 72
OCT 107
NOV 49
DEC 48
JAN 64
FEB 30
MAR 46
APR 126
MAY 173
JUN 120
JUL 125
EMPTY STOMACHS
0
20
40
60
80
ALGAE
0
20
COELENTERATES
NONE
POLYCHAETES
0
20
40
COPEPODS
0
20
STOMATOPODS
NONE
MYSIDS
0
20
IDOTHEA RESECATA
0
20
40
OTHER ISOPODS
0
20
AMPHIPODS
0
20
40
CAPRELLIDS
0
20
40
60
PISTOL SHRIMP
0
20
TOTAL SHRIMP
0
20
OTHER SHRIMP
0
20
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CRABS
0
20
40
60
CEPHALOPODS
0
20
(CONTINUED)

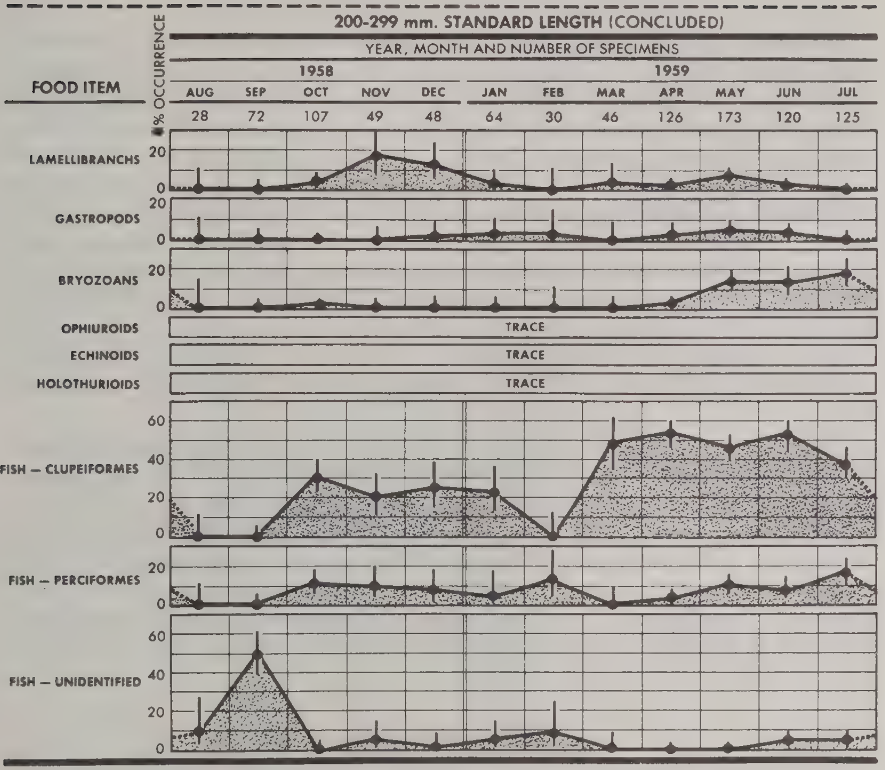


FIGURE 26. Food of 200–299-mm kelp bass. Data from specimens collected by hook-and-line and spear from the San Diego region except for February, 1959, in which specimens were from the San Benito Island (lat. 28° N.).

300–399 mm Fish (Figure 27)

Frequencies in general resemble the smaller class. Fishes made an important contribution during all months. Perciform items included flatfish, topsmelt, pipefish, and embiotocid, one goby, one small "giant" kelpfish, and a labrid. Small items, such as polychaetes, gammarid amphipods, and caprellids, continued to be taken, but at low frequencies.

Small pieces of kelp were quite common in this and succeeding sizes of bass. Because kelp bass are carnivorous and the algae never showed any evidence of being digested, it seemed probable that the "kelp-perch sized" fragments were mistaken for prey. Samples of this nature originated from sportfishing boats, and considerable quantities of kelp are sometimes fragmented by the propellers in the process of "chumming" and anchoring at a fishing site.

Fish 400 mm and Larger (Figure 27)

Fish and *Macrocystis* fragments predominate in the samples, and small invertebrates are nearly absent. Cephalopods (mainly octopus) were important. Giant kelpfish predominated among the perciform fishes, followed by blacksmith, and señorita; topsmelt, flatfish, cottids, rockfish, and pipefish were less frequent. The data are too few to indicate possible seasonal feeding peaks.

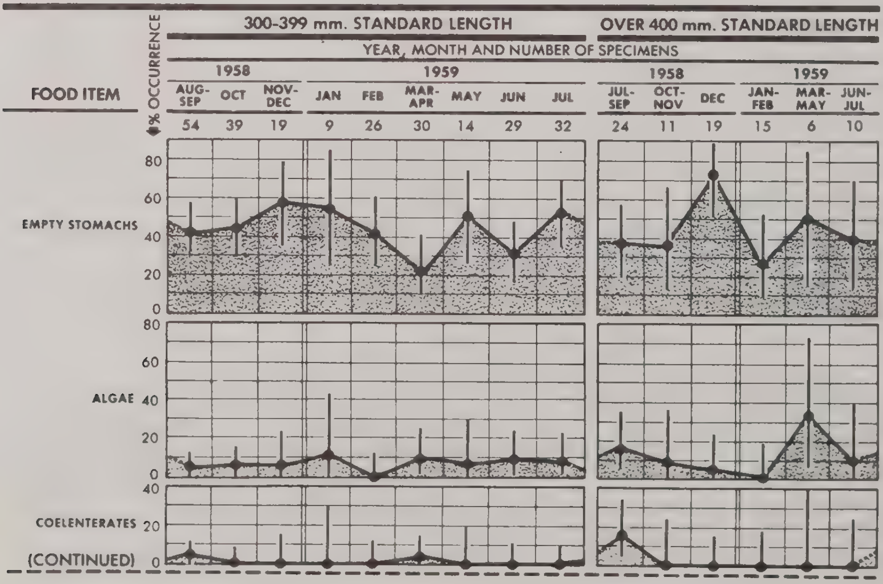
General Conclusions Regarding Diet

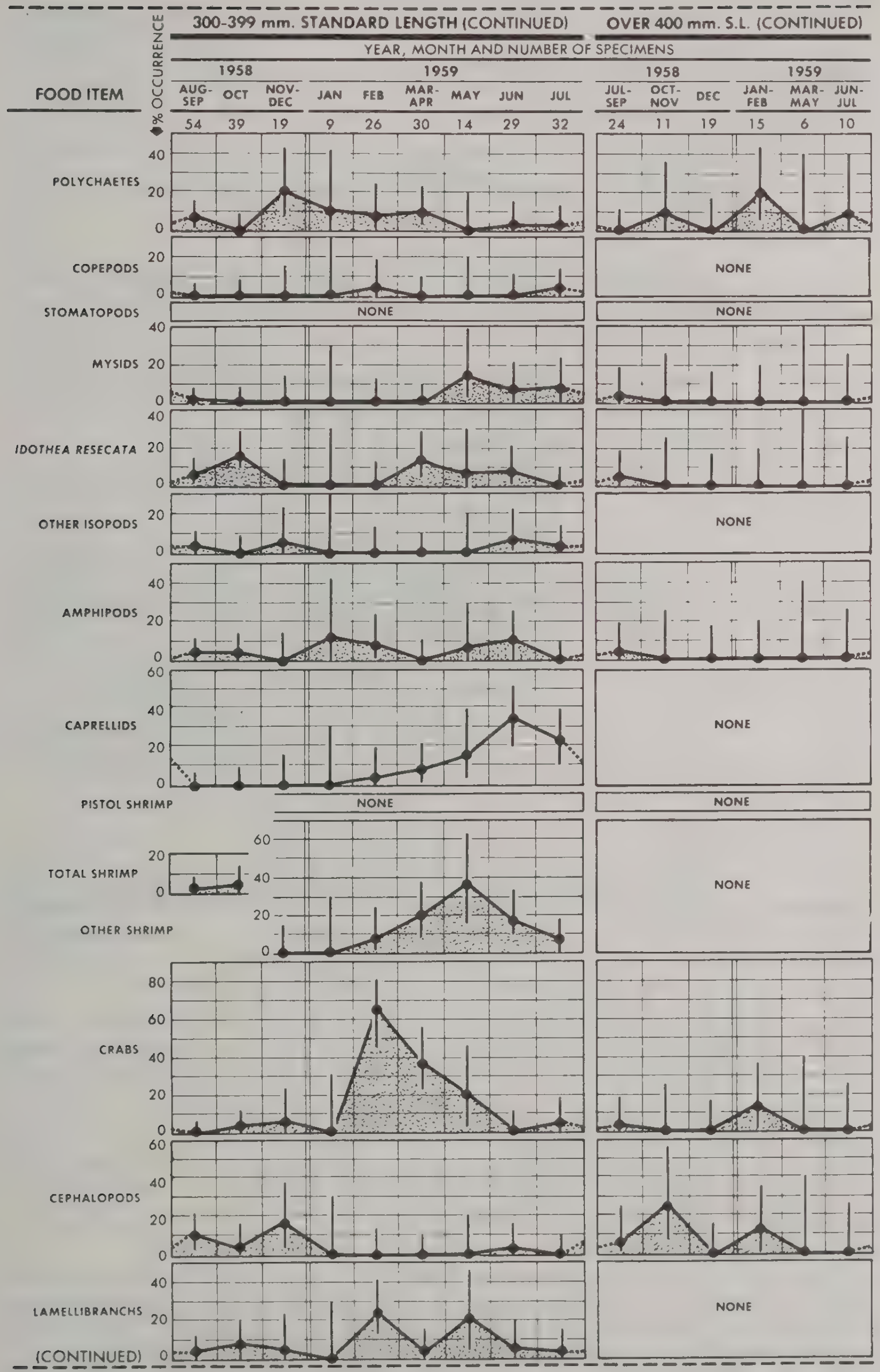
The kelp bass is apparently a generalized carnivore and utilizes a broad spectrum of the available foods. Judging from food frequency figures and the derived Table 26, there is a selection of larger, more motile prey, mainly fish and cephalopods, as the fish grow larger. Very small foods sometimes occur, however, and it is difficult to understand how the effort required to pick caprellids from kelp fronds may be rewarding to a fish as large as 200 mm SL. Similarly, solitary polychaetes shorter than 5 cm were taken by individuals 400 mm and larger, but cannot have been very rewarding at the low concentration at which the food organisms were observed. Also brine shrimp approximately 3 mm long were individually taken by a well-fed and actively growing aquarium held specimen of 115 mm TL. Probably these feeding activities represent relicts of earlier patterns in the fish's development.

In terms of the general categories, the kelp bass diet remains broad up to the largest size-class, at which time it becomes more limited. The averages for number of food categories utilized by the size-classes are 9.7 for 100–199 mm, 11.4 for 200–299 mm, 10.9 for 300–399 mm, and 5.2 for fishes 400 mm or larger. Considerable food variety is, however, available within each category and the general data give no indication of breadth of utilization within the categories. Such an analysis requires that all items be identified to species, which was judged too time-consuming for the present study.

REPRODUCTION

The spawning season was first delineated by Clark (1933) as June, July, and August on the basis of specimens examined at the San Pedro commercial fish markets. She indicated the smallest size at maturity to be approximately 25 cm TL and that larger fish mature earlier than smaller ones. Collyer and Young (1953) found that some kelp bass





mature as early as April and also that a few smaller than 25 cm mature. In other respects their findings substantiated those of Clark.

Two methods were used for assessing maturity in the Kelp Program studies. Davies' (1956) subjective maturity categories (inactive, active, ripe, ripe and running, and spent) were recorded as fish were

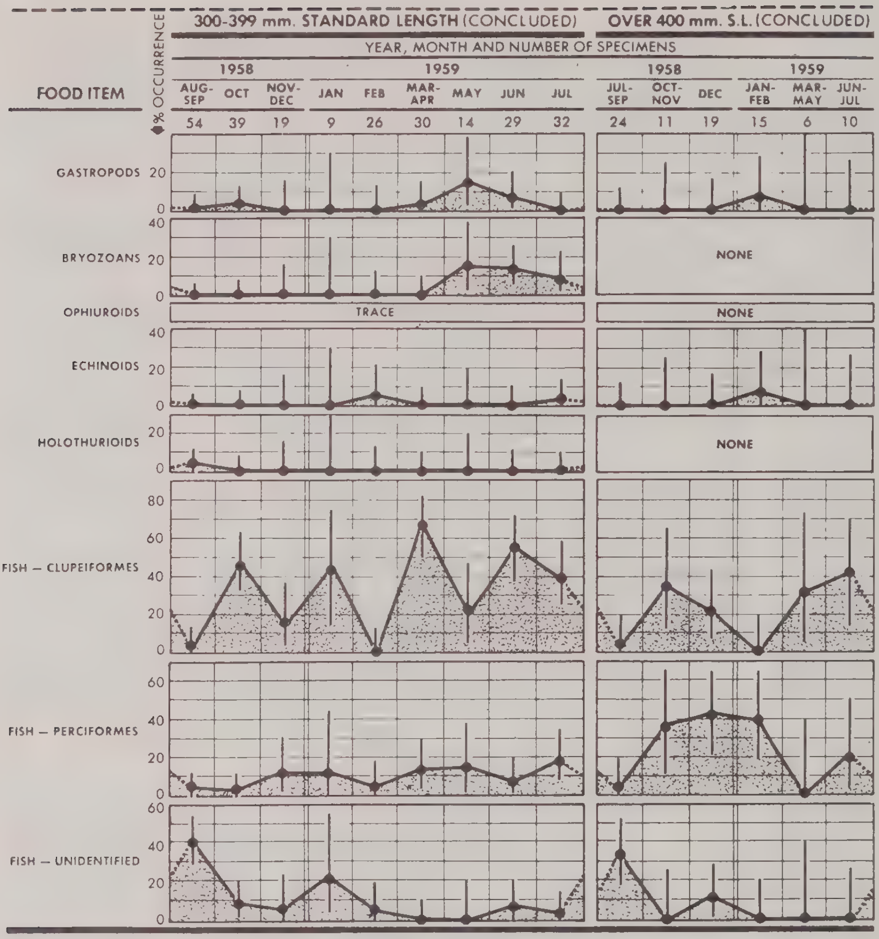


FIGURE 27. Food of 300–399 and 400 + mm kelp bass. Data from specimens collected by hook-and-line and spear from the San Diego region except for February, 1959, in which all specimens were from the San Benito Islands (lat. 28° N.).

gutted aboard sportfishing boats. Volumetric displacement was also taken on all gonads in the laboratory at the time the gut contents were examined. Volumetric displacement was converted to weight by assuming that 1 cc equaled 1 gram, considered approximately correct on the basis of weight-volume comparisons. Of the two methods, the volumetric analysis was more valuable because it included more specimens and a greater size-range of samples (fish approximating or smaller than the 12-inch (300 mm) legal size were not gutted aboard the ship, but were preserved entire).

Graphical analysis of breeding condition (Figure 28) demonstrates that larger fish of both sexes mature earlier, are mature longer, and are mature in a greater percentage within the samples than smaller fish. Data for the largest females, are insufficient to determine whether the scattered points for June through September represent one or two modes; hence two spawning peaks may be indicated. Maturity evidence based on gonad weight as a percentage of whole body weight (Figure 29) agrees closely with the subjective data. The midrange analysis of

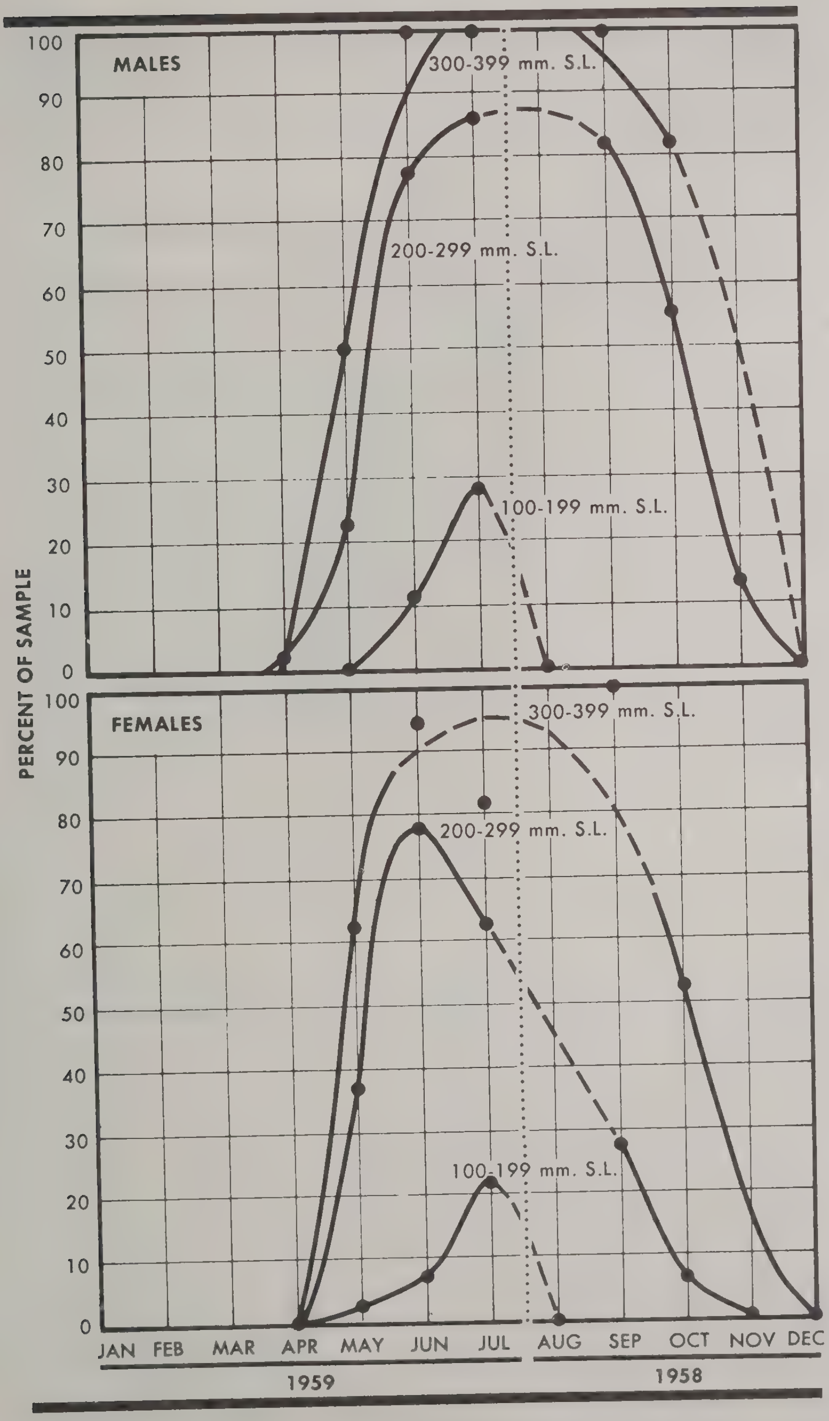


FIGURE 28. Percentages of kelp bass of all sizes in ripe condition (August 1958 through July 1959). Monthly sample sizes, 3–87 specimens.

Figure 29 (midrange is used because the data are not normally distributed within the months) shows peaks in gonad volume in June for all females and for the largest males. The short and broad peaks for males 200 and 250 mm long, compared to males larger than 300 mm, suggests that the largest males spawn more consistently in June.

TABLE 26

Relative Status of the Seven Most Frequent Dietary Items for Size-Classes of *Paralabrax clathratus*

Values in weighted percentages within each size-class. Seven most frequent items underlined. Values increased with utilization.

Item	100–199 mm.	200–299 mm.	300–399 mm.	400+ mm.
Pistol shrimp	7	4	0	0
Idothea resecata	7	7	4	2
Caprellids	8	6	5	0
Other shrimp	8	7	5	0
Amphipods	7	6	5	2
Crabs	11	9	7	5
Clupeiformes	10	14	14	20
Polychaetes	4	7	6	8
Lamellibranchs	4	4	7	0
Fish, unidentified	5	5	7	8
Algae	2	5	7	15
Perciformes	4	5	8	20
Cephalopods	0	1	4	8

Relative gonad volume varies as much as three fold within the size-classes. Some of this variation is undoubtedly attributable to sources of errors in measurement, such as incomplete removal of gonads at time of gutting, sex products lost from ripe fish, and erroneous readings at the time of volumetric determination (several extreme and atypical readings ascribed to operator error were eliminated from consideration). Some variation may have arisen from the condition of the fish, although all appeared well fed and healthy. Probably the major part of the large variation found was caused by fish releasing only a portion of the sex products during any single spawning act. This would result in similar-sized fishes having various degrees of gonad fullness. Supporting evidence is derived from the fact that frequencies for ripe fish (Figure 28) remained high from July through September while gonad-volume declined (Figure 29). If sex products are completely released at spawning, the minimum value for gonad volume should be attained by some fish near the onset of spawning season, but this hypothesis is contradicted by data on the range of percentages (Figure 30).

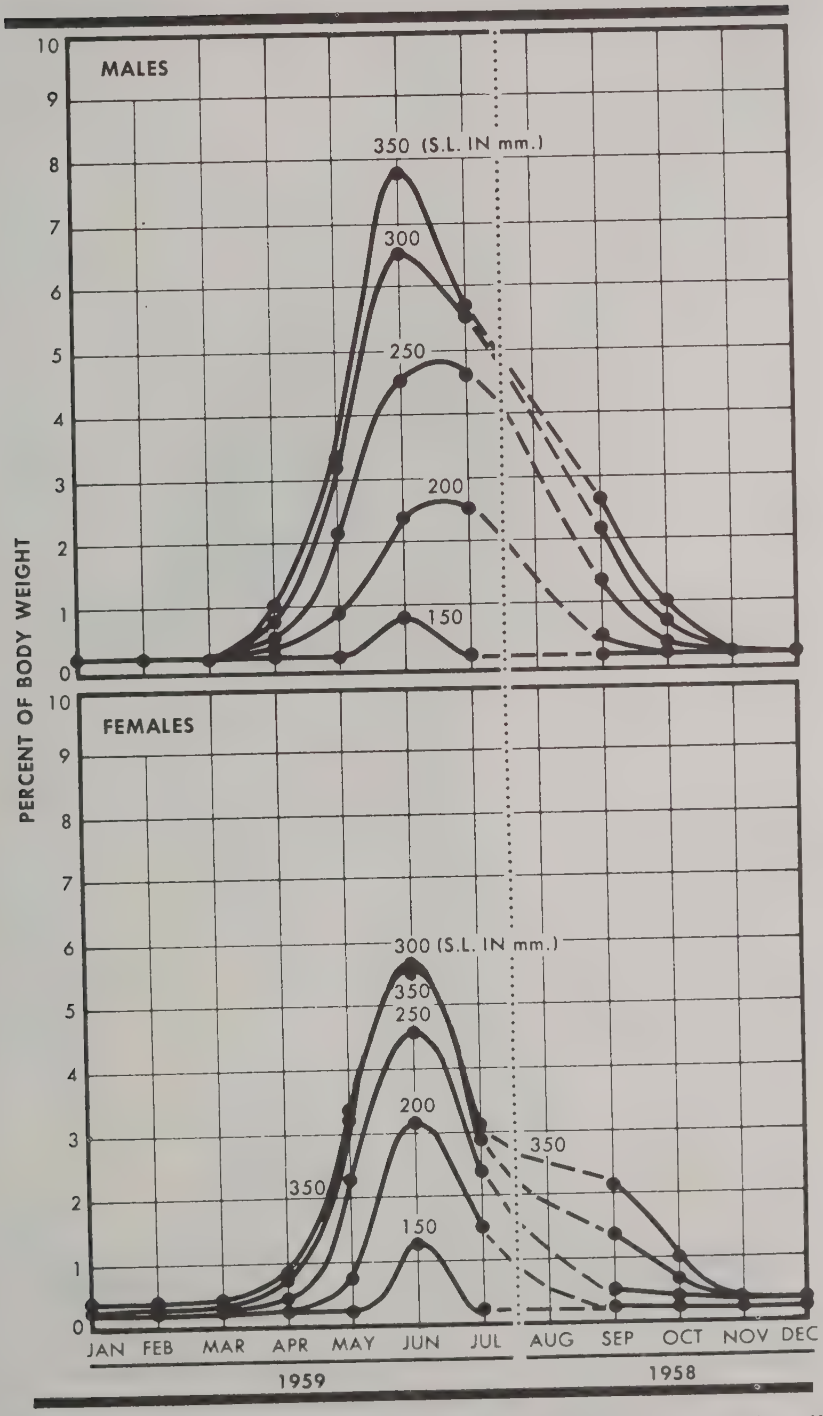


FIGURE 29. Midranges of gonad weights for selected standard lengths of kelp bass. Years transposed to illustrate trends.

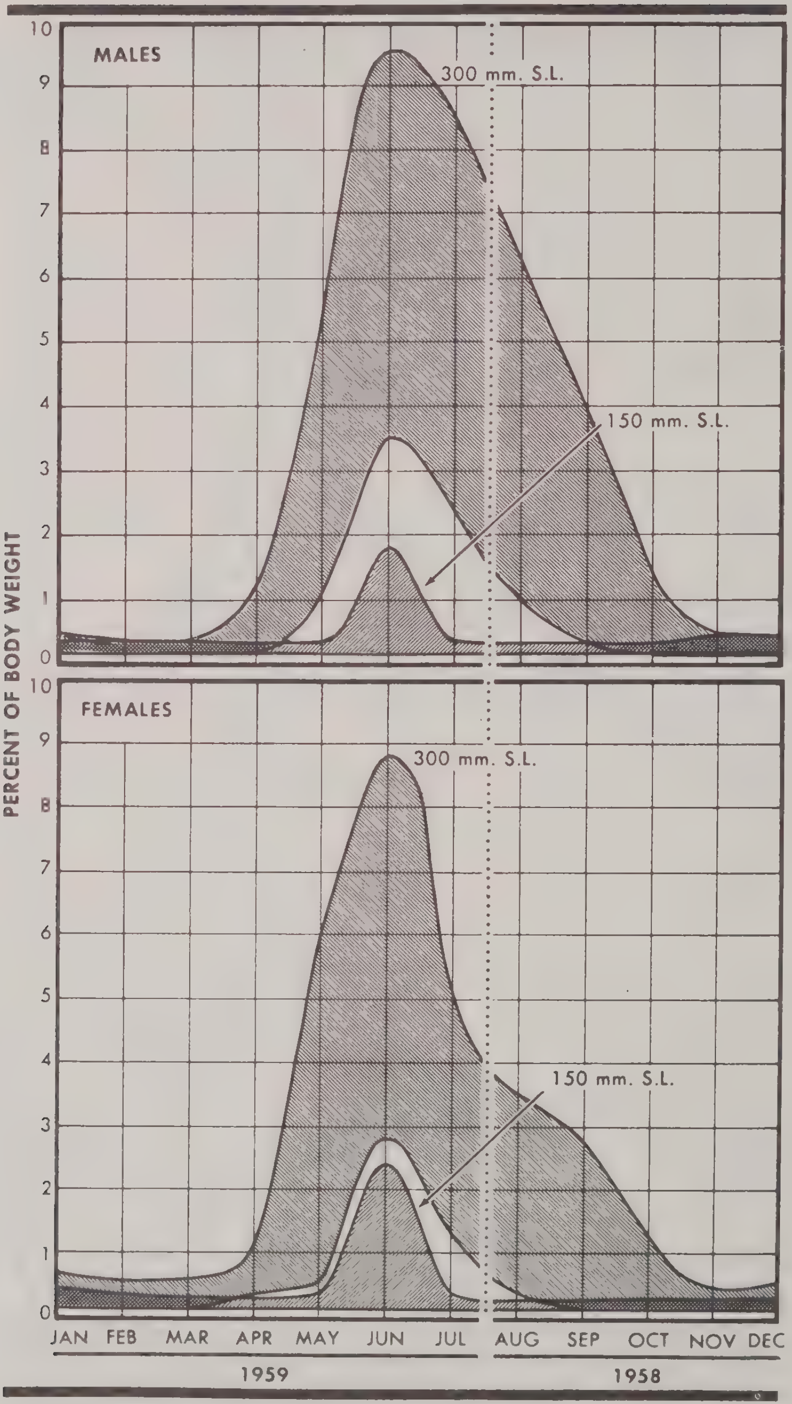


FIGURE 30. Seasonal variation in gonad weight for large and small adult kelp bass. Shaded areas are ranges in percentage of body weight. Years transposed to illustrate trends.

No sudden spawning of the entire population is indicated, such as that described for *Perca fluviatilis* by Le Cren (1951).

The relationship between body size and maximum gonad volume is characterized by extreme allometry. The regression of maximum gonad volume on fish length for 140 to 178 mm specimens at the peak of breeding season (May, June, July) approximated log Weight = 18.9 log Length —41.8. For larger fish the slope of the regression declined steadily with size increase and formed a shallow curve with a slope of approximately 3.0 for specimens 270 to 300 mm long (for such a slope the increase in maximum gonad size is approximately proportional to increase in body weight). The slope then declined to approximately 1.21 at 400 mm. The significance of the abrupt change in slope near 178 mm is not certain, but this is the approximate length at first maturity, reached at the end of the second year. A slope exceeding 3.0 (or the cube) up to 270–300 mm indicates reproductive potential exceeding body-weight increase. At sizes greater than 300 mm the relative increase in reproductive potential declined and at 400 mm was proportional to length increase only (or the cube-root of weight increase). These relationships were very different from those in *Perca fluviatilis,* for which Le Cren (1951) stated "although there is some individual variation in the gonad: body-weight ratio, it tends to be constant at any one season for all sizes of fish of the same state of maturity." During the breeding season some males became golden on the snout. This color was most prominent in small adults during June and July, and appeared to be more dilute in large specimens. Occasionally, some large males also are prominently marked; several were seen at 60- to 70-foot depths with golden coloration sufficiently intense to be noted from several yards away.

Although numerous dives were made during the spawning season, no obvious spawning behavior by kelp bass was ever observed. Limbaugh (1955), however, saw several spawning aggregations and noted:

> "The ripe adults tend to aggregate during spawning activities, usually in the kelp in relatively deep water. Hundreds of kelp bass and other fishes may aggregate in a small area while spawning goes on. Both ripe females and males have been taken from such aggregations. Ripe sand bass have also been found in these groups. The other fishes attracted to the activity include sargo, pileperch, kelpperch, blacksmith, señorita and sheepshead."

OBSERVATIONS ON THE POINT LOMA FISHERY

Description of the Area

Pt. Loma is a high, narrow peninsula extending approximately 4 miles south of Ocean Beach, in San Diego. An extensive and relatively shallow shelf extends along the entire ocean side of the peninsula outward to an escarpment, at 50-60 feet depths, parallel to the coast and about 1 mile offshore. Although the shelf had supported considerable beds of kelp, the stand during the study was only a small fraction of the former standing crop. The underwater shelf is quite flat, but occasionally, considerable topographic relief is provided by rectangular boulders, in areas that vary in extent from several square feet to nearly an acre. Several areas of high relief (such as one called

New Hope Rock) are composed of flat surface bedrock overlain with desk- to house-sized rock outcrops that are heavily undercut and sometimes perforated by caves or channels. The cliff that terminates the platform on the ocean side was evidently a sea cliff during the lower sea levels of earlier geological periods.

Sportfishery of the *Mascot III*

Catch statistics for 1958 and 1959 were from the *Mascot III*, the only party sportfishing boat that consistently exploited the kelp-bass fishery in the Pt. Loma beds during the studies. Its operations were confined almost exclusively to this fishery. It accounted for an estimated three-fourths of the total take of kelp bass off Point Loma, including that by private boats. Some supplementary data were obtained from the La Jolla sportfishery, 10 nautical miles to the north.

The *Mascot III* was 65 feet long, of wood construction, and diesel-powered. Two large bait wells near the stern were loaded with live anchovies or sardines prior to a fishing trip. The boat made two trips daily between March and October, and some half-day trips during the remaining months. Stomachs and gonads were sampled weekly from kelp bass caught aboard the vessel. Three fishing sites were heavily utilized by the *Mascot III*. According to the skipper, the preferred sites are near points of the kelp bed projecting seaward, or in small ''bays'' along its outside edge. One site yielded large numbers of bass quite consistently, and was visited daily during several months in the spring. It continued to yield adult bass in quantity over periods of several weeks during summer and fall. The skipper estimated that a minimum of 200 fish were taken weekly from this site during a 2-month period in the spring. This weekly take was far in excess of the normal standing crop assayed at any site by belt transect or by wall net.

Sites were located by landmarks on the shore and by the fathometer. It was customary before anchoring to throw live anchovies in the ship's wake to establish a chum line that attracted fish to the boat. Chumming usually continued intermittently while the site was fished.

Definite preference was shown for sites near moderate to heavy kelp, although certain locations a half mile or more from the beds sometimes yielded large fish in considerable quantities. One very productive site, a point of kelp projecting seaward near the submarine escarpment, was inspected by SCUBA. The bottom there is at 80 feet and consists of fragmented rock with numerous crevices. Similar favored fishing sites near La Jolla kelp beds, also investigated by SCUBA, all have rocky bottoms with considerable relief.

Although kelp bass are available to the sportfishery at any season, the *Mascot III* normally operated between late March, or early April, and October or November. Length of season depended on the weather and passenger demand. Heaviest passenger loads normally occurred on weekends and business was at its best from June to September, when schools were vacant and tourist traffic high.

Catch per unit effort (fish per fisherman per half day) varied considerably from June through October 1958. Passengers averaged two to six bass during June, but the catch declined during July and reached lowest values (approximately 0.5) during the first 2 weeks of August. Fishing improved between late August and early September to approximately 2.0, after which (September 10-13) it declined again to 1.0. Catch then increased abruptly to 5.0 on September 15, and to 5.5 on September 24. During October averages declined below 2.0.

The seasonal fluctuations in catch per unit effort were puzzling, but did not appear to be random. Records of tides, weather, lunar phases, surface temperatures, and captures of other sportfishes kept concurrently on the vessel showed no important correlation with the fluctuations. Spawning condition of the kelp bass may be significant. The high average catch per unit effort during June (despite heavy passenger loads, which tend to lower the average) corresponded to the peak in breeding during that month.

Deflections in the curves for females during late August and early September corresponded to the second period of high catch per unit effort. The short-term highs in fishing success during mid- and late-September might have been caused by low passenger loads after public schools convened in the fall, discussed below.

Number of passengers on the boat must be considered when passenger catch per unit effort is analyzed. Catch data for the *Mascot III* indicated an inverse relationship between passenger load and fishing success (Table 27). Under crowded conditions passenger fishing areas overlap, with resultant gear interference. Also, crowding usually occurs on weekends and holidays when there is a higher proportion of novices. Experienced fishermen normally attempt to avoid the crowded weekend trips.

TABLE 27

Variation in Average Kelp Bass Catch per Unit Effort with Passenger Load

Data taken on the sportfisher *Mascot III* for the months May, June, and July 1958.

Number of passengers per trip	Frequency	Average catch per unit effort
0–4	8	6.1
5–9	35	4.7
10–14	23	2.5
15–19	15	2.7
20–24	20	1.9
25–29	17	2.7
30–34	15	1.8
35–39	13	2.1
40–44	6	1.9
45–49	7	1.0
50–59	3	1.0

Yield and Mortality for the Population

Yield of kelp bass for the Pt. Loma region during 1958–1959 was estimated from the *Mascot III* log sheets and from length-frequency data obtained from the catch. Nearly all bass taken, including the undersized, were examined and measured. Because weight vs. length measurements involved fresh weight for the legal fish and preserved weight for the undersized, weight change with preservation was measured. In 10 fish of three species, including *P. clathratus,* a preservation period of 2 weeks in four-percent formaldehyde resulted in a maximum individual gain of 3.1 percent and a maximum loss of 0.5 percent. Average change for the group was a gain of 1.0 percent, a difference judged negligible.

To determine weight-length relations 150 specimens 65 to 245 mm SL and 8 specimens 255 to 615 mm long were utilized (Figure 31). The regression of weight on length in the smaller fish, calculated by the least-squares method, was:

$$\log \text{Weight} = 3.256 \log \text{Length} - 5.178$$

which was similar in slope to a regression for all sizes calculated by Parke H. Young (personal communication). The data for the larger bass gave a slope of 2.725. The marked decrease in slope for the larger fish may reflect the decrease with growth in maximum relative gonad size, as noted previously.

An estimate of total weight of kelp bass taken by the *Mascot III* between July 1958 and July 1959 required both an estimate of the average weight of fish and the total number of fish taken. An average weight of 952.8 g was obtained by converting the size-frequencies observed during the sampling period (Figure 32) to weight-frequencies by the weight-length regressions. The *Mascot III* catch returns indicate that 17,026 kelp bass, weighing 18 tons, were taken during the study period.

By measuring the area between 1 and 15 fathoms on a contour chart of the Point Loma shelf (the northern and southern limits must be somewhat arbitrarily defined but have some basis in the extent of rocky habitat), the area from which the bass were taken is estimated, as a minimum, to be 3.17 square miles or 2,030 acres. On this basis, the annual take for the *Mascot III* is estimated to have been approximately 16 pounds per acre. On the assumption that the *Mascot III* catch constituted approximately three-fourths of the kelp bass taken in the Point Loma vicinity, the minimum annual yield between July 1958 and July 1959 is estimated to have been 21 pounds per acre.

Total mortality for the kelp-bass population was estimated from the size-class frequencies (Figure 32) and from the age and growth data presented by Collyer and Young (1953). Their values were converted from inches total length to millimeters standard length by a plot of duplicate measurements taken on laboratory specimens (Figure 33). Size-class frequencies for sampling periods during the year (Figure 32) were smoothed twice over three points, and intercepts for the various age classes (summer lengths) on the smoothed frequency plot were obtained by a Walford plot of the growth data (Table 28). The intercepts represented theoretical frequencies for the various age-classes and gave an estimate of decline of year classes with time, or mortality, when plotted logarithmically. A visual fit of the regression data (Figure 34) indicated that the population experienced an average mortality of approximately 42% during the years prior to the study.

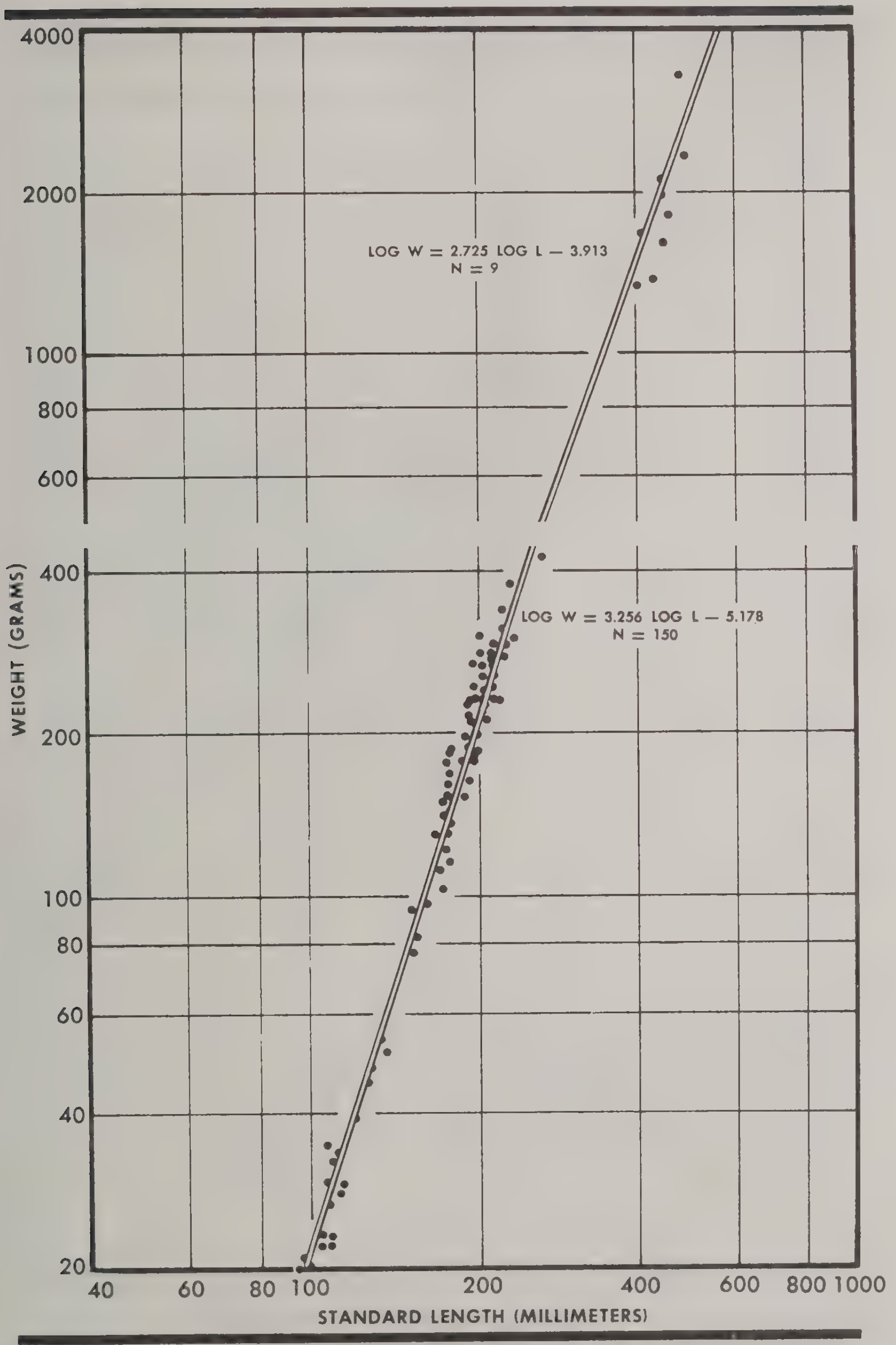


FIGURE 31. Regressions of weight on length for kelp bass from the La Jolla and Point Loma kelp beds. Upper line fitted by eye, the lower by least-squares.

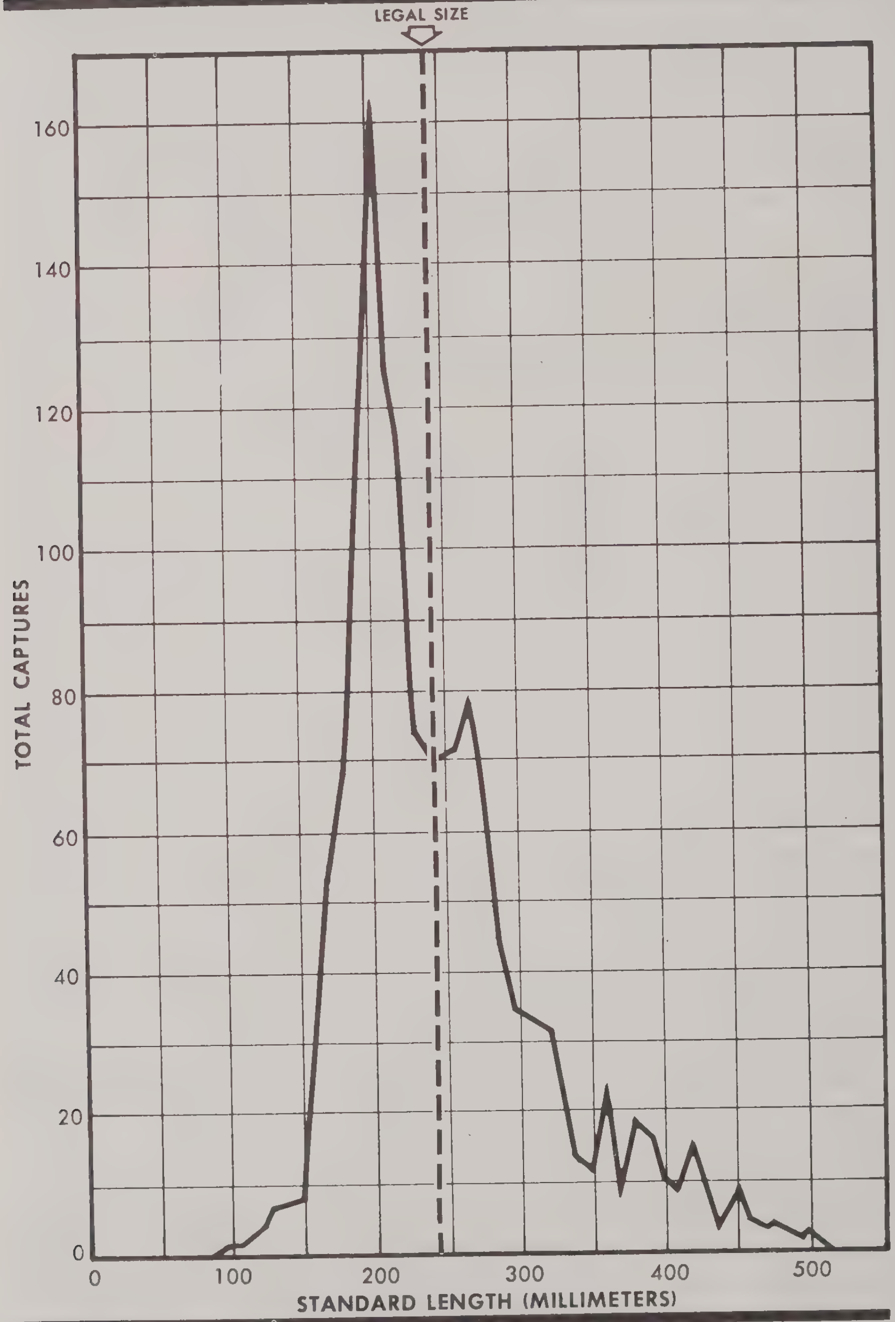


FIGURE 32. Cumulative size frequencies of kelp bass taken aboard the *Mascot III*.

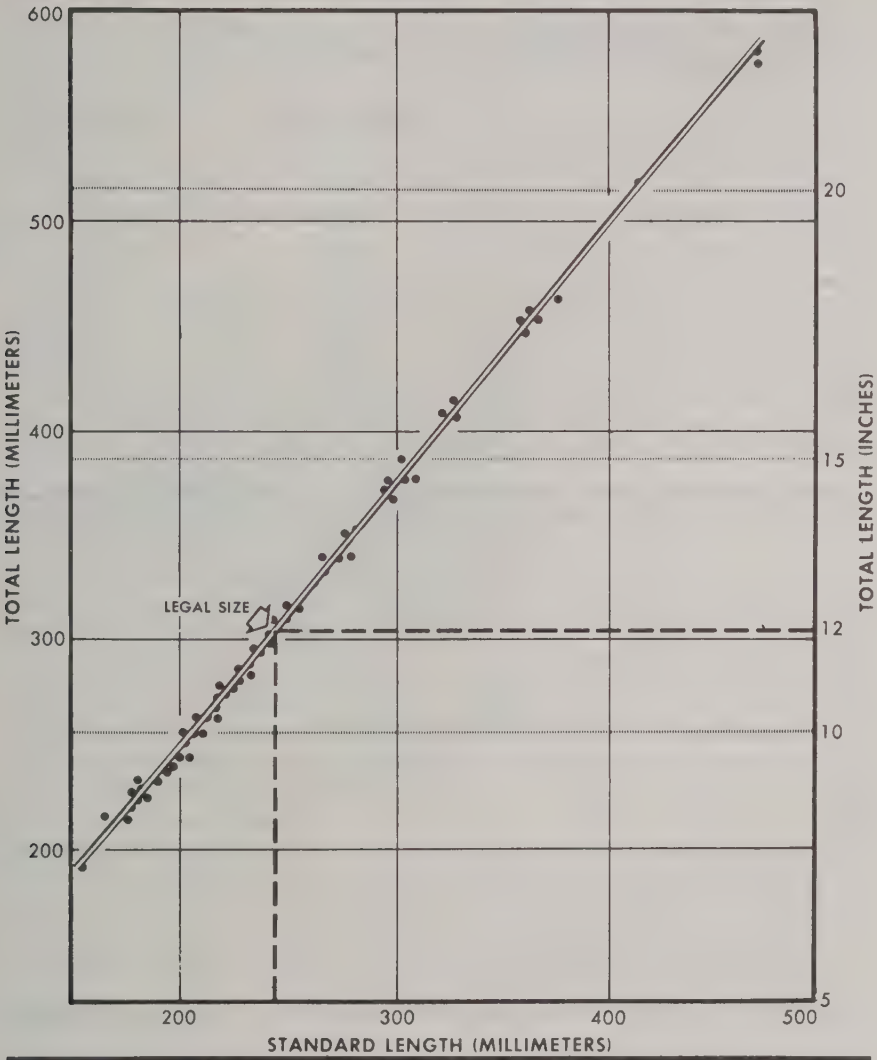


FIGURE 33. Relationship between total length in inches and standard length in millimeters for the kelp bass.

TABLE 28

Theoretical Size and Frequency of Kelp Bass of Various Ages in the Point Loma Sportfishery During the Year July 1958–July 1959

Age (years)	Midpoint of size class at age (mm)	Observed frequency (smoothed)
1	80.0	0.5
2	149.8	10.5
3	210.8	118.0
4	264.1	58.6
5	311.1	29.5
6	351.7	11.0
7	387.3	8.0
8	418.4	7.0
9	445.7	4.0
10	469.8	2.5
11	490.7	1.0
12	508.6	0.5
13	524.4	0.0

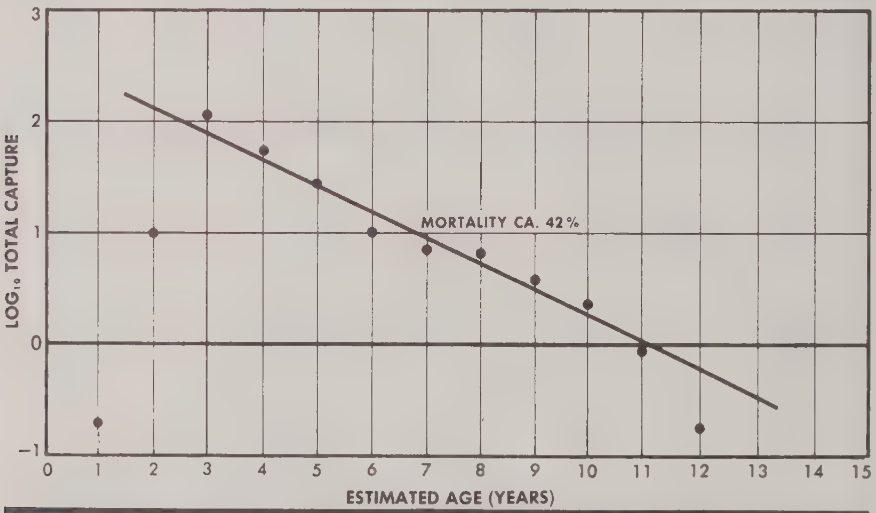


FIGURE 34. Estimated mortality for kelp bass in the Point Loma sport-fishery prior to 1959, based on specimens taken during the study. Regression fitted by eye.

SUMMARY

1. The kelp bass is an important demersal sport fish that is common in the rocky inshore zone of southern California and Baja California, and nearby islands.

2. A principal habitat requirement is some type of bottom relief, such as rock, plants, or debris. A rocky substrate is not an ecologic necessity providing that kelp or some other form of cover is present.

3. Although adults occur from the intertidal zone to nearly 200 feet, the greatest proportion of the population remains shallower than 100 feet.

4. The most consistently encountered species on the SCUBA surveys was the kelp bass. It was not, however, the highest in numerical abundance.

5. Adult bass probably move into the more attractive areas as the original inhabitants of these areas are removed by fishing.

6. Individuals become more cautious and probably occupy larger territories with growth.

7. Individuals are noticeably wary when objects align with them, a reaction presumed to be of protective advantage.

8. Although no interspecific or intraspecific aggression was noted in the field, an aquarium-held specimen displayed a variety of aggressive postures and actions against another species.

9. Calculations of home range from data of Limbaugh (1955) indicate a maximum radius of approximately 1175 feet for adults. This value undoubtedly varies considerably with size and the terrain.

10. Approximately 1,700 specimens, mostly caught by sportfishing boats, were examined for food contents.

11. On the basis of the food studies, it is concluded that the kelp bass is a medium-sized predator and that the adults are near the top of the inshore food chain. Intermediate-sized, usually vagile, prey items are taken. Young fish utilize small demersal crustaceans. As fish grow the diet shifts to larger prey, such as fish, squid, and octopus.

12. Two feeding peaks occur during the year, the first in spring, immediately prior to breeding, and the second in fall, at the end of the breeding season.

13. Gonads of large adults begin to enlarge in April, and those of all adults attain maximum size in June. The volume then decreases slowly until the end of the breeding season in November. Relative gonad volumes become disproportionately large in adults to a standard length of 300 mm, then decline sharply. Larger adults remain in breeding condition longer than younger ones.

14. Some male kelp bass become sexually colored during the breeding season by developing a golden region on the snout. Coloration is usually most prominent and consistent in the smaller adults, but some large adults also are conspicuously colored.

15. The sportfishery at Point Loma, San Diego provided information on the biology of the kelp bass.

16. Passenger catch per unit effort varied with the number of persons aboard the sportfishing boat as well as with their skill. Spawning condition of the fish may be associated with catch per unit effort.

17. A yield of approximately 21 pounds per acre per year was calculated for the Point Loma kelp-bass fishery for the period immediately preceding the study.

18. Total mortality for the kelp-bass population at Point Loma was estimated at approximately 42 percent.

References for this paper follow reprint no. 131
in this volume.

8. OBSERVATIONS ON THE FOOD OF THE KELP-BED FISHES

JAY C. QUAST
U.S. Bureau of Commercial Fisheries
Auke Bay, Alaska

INTRODUCTION

Data on the diets of southern California inshore fishes are scattered and incomplete. With the exception of Limbaugh's (1955), most studies have involved few specimens, a limited number of species, and restricted habitats, and have employed sampling methods that could have resulted in misleading data. Several studies involve only one sample taken at one place at one time of year. Frequently the samples were not broken down into size-classes of fish, despite *a priori* knowledge that fish diet changes with growth. Knowledge of food availability remains crude, and actual food preferences can only be guessed. Life histories of important prey invertebrates are undescribed.

In this section published data on the diets of southern California rocky inshore fishes are summarized, and supplemented by information from the Kelp Program research. Literature sources include Metz (1912), who examined some intertidally collected fish specimens for food, and also described their visceral anatomy; Mitchell (1953), who also studied intertidal specimens, but whose small collection was made with rotenone, introducing possibilities of considerable bias; Limbaugh (1955), who examined subtidal specimens taken by spear over a 5-year period (his work includes biological and ecological notes, but unfortunately does not give number and size of specimens examined); and Fitch (1960) and Baxter (1960), who presented additional information on food and biology, but borrowed heavily on Limbaugh and did not give sampling data.

ACKNOWLEDGMENTS

The studies were concurrent with those for the kelp bass (see Chapter 7) and the same persons gave their assistance. Nearly all food data were based on examinations by H. George Snyder. Charles T. Mitchell constructed preliminary drawings for the food figures. The research was supported principally by the State of California Department of Fish and Game, and in part by the Institute of Marine Resources, University of California.

METHODS

Approximately 1700 kelp bass and 500 representatives of other species were examined for food items. Each collecting method introduced its own bias and it was not practical to eliminate even the more obvious types. Foods from specimens taken on sportfishing boats contained high percentages of the northern anchovy, *Engraulis mordax,*

Reprinted from California Department of Fish and Game,
Fish Bulletin 139, 1968.

because this species was used nearly exclusively for bait. Variable proportions of fishes from the wall-net collections, described in Chapter 6, probably fed on dying crustaceans before the fish themselves were affected by rotenone poisoning. Fishes taken by spear frequently had to be chummed with crushed sea urchins, so echinoderm percentages were too high in these samples. The data are nonetheless regarded as reasonably representative but care should be taken in interpretation. Identifiable bias sources are noted. The inclusion of intestinal food data adds additional weight to the truly representative foods. Differential digestion rates for different items are not regarded as an important source of error.

The entire digestive tract was examined because intestinal items could usually be identified at least to a higher taxon. Food data are presented by frequency-of-occurrence (Figures 35 to 49). The 90-percent confidence limits (Tate and Clelland, 1957), are not presented for the purpose of actual significance tests, but rather as graphical indications of relative reliability.

FINDINGS

California Moray, *Gymnothorax mordax* (Figure 35)

All 19 specimens used were from a morning poison collection off Bathtub Rock, near Scripps Institution of Oceanography, in July 1959. Bottom was mixed sand and rock at 25 feet. Specimens displayed two size-frequency modes at 185 and 220 mm SL; all but three were shorter than 240 mm.

Shrimp and crab were principal dietary items, and the few data agreed with Limbaugh's finding (*l.c.*), that crustacea and small fish are heavily utilized. Red rock shrimp, *Hippolysmata californica*, thought by Limbaugh to be a cleaning organism (personal communication), were found in traces in both studies. Abalone represent a potential if not actual food, because morays are easily lured from crevices or caves during daylight when abalone are overturned. Data on nine tropical *Gymnothorax* species collected by Hiatt and Strasburg (1960) agreed closely with our findings on the California moray.

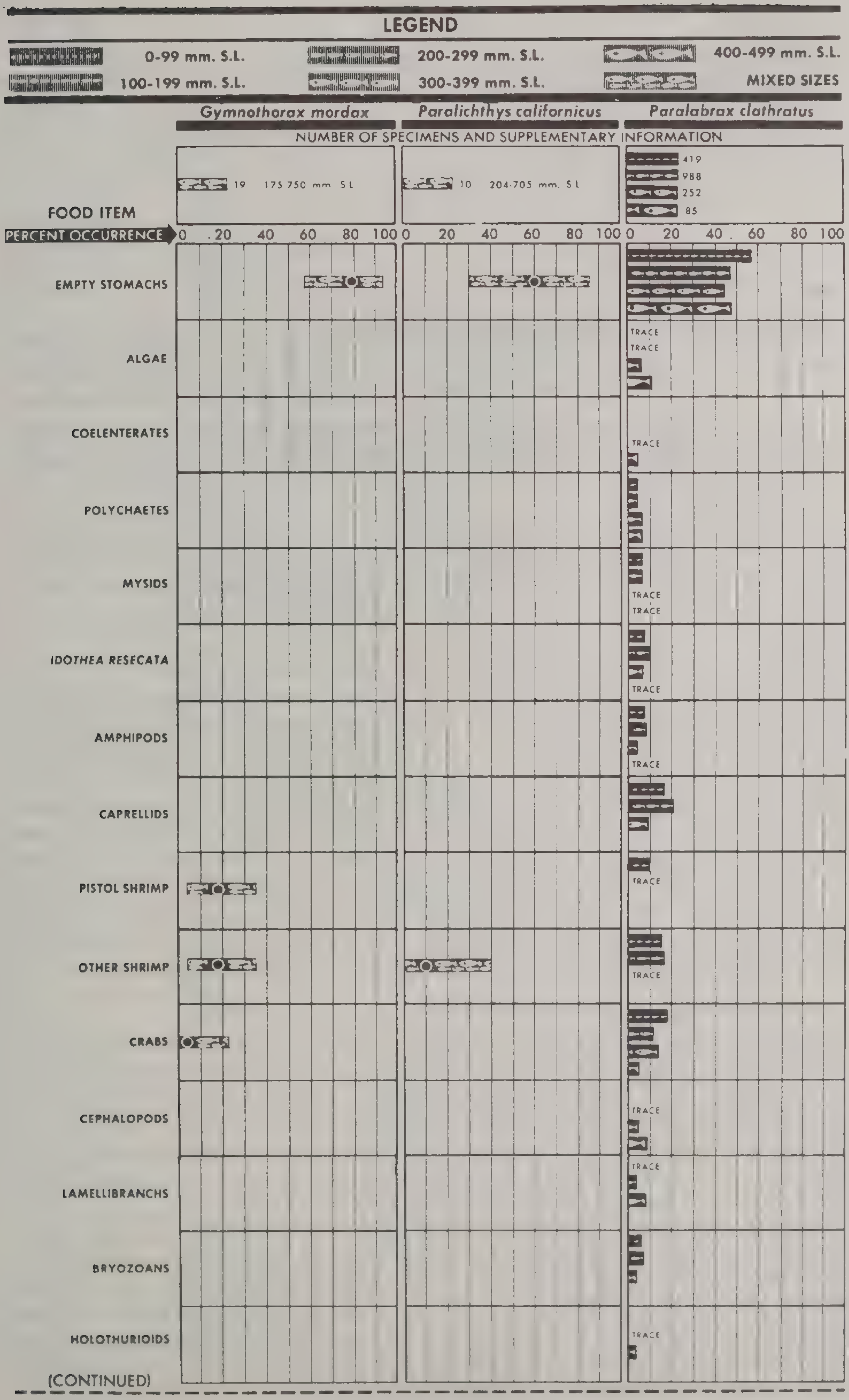
California Halibut, *Paralichthys californicus* (Figure 35)

Individuals were infrequent in kelp beds, but some dietary data were obtained. All specimens used were speared individually during spring and summer seasons over sand bottom at 30 to 80 feet. An almost completely piscivorous diet is indicated. Remains of engraulids, atherinids, and small flatfish were identified, similar to the findings of Limbaugh (*l.c.*).

Kelp Bass, *Paralabrax clathratus* (Figure 35)

This species is discussed in detail in Chapter 7, and only a summary is presented here. All seasons were represented. Since the majority of specimens used were from sportfishing boats, the values for clupeiform fishes probably are artificially high. Because of large samples, the 90-percent confidence limits were very narrow, and are not indicated.

Young fish fed principally on such demersal crustaceans as amphipods, spider crabs, and pistol shrimp. With growth, the food shifted


LEGEND
0-99 mm. S.L.
200-299 mm. S.L.
400-499 mm. S.L.
100-199 mm. S.L.
300-399 mm. S.L.
MIXED SIZES
Gymnothorax mordax
Paralichthys californicus
Paralabrax clathratus
NUMBER OF SPECIMENS AND SUPPLEMENTARY INFORMATION
19 175-750 mm. S.L.
10 204-705 mm. S.L.
419
988
252
85
FOOD ITEM
PERCENT OCCURRENCE
0 20 40 60 80 100
EMPTY STOMACHS
ALGAE
COELENTERATES
POLYCHAETES
MYSIDS
IDOTHEA RESECATA
AMPHIPODS
CAPRELLIDS
PISTOL SHRIMP
OTHER SHRIMP
CRABS
CEPHALOPODS
LAMELLIBRANCHS
BRYOZOANS
HOLOTHURIOIDS
TRACE
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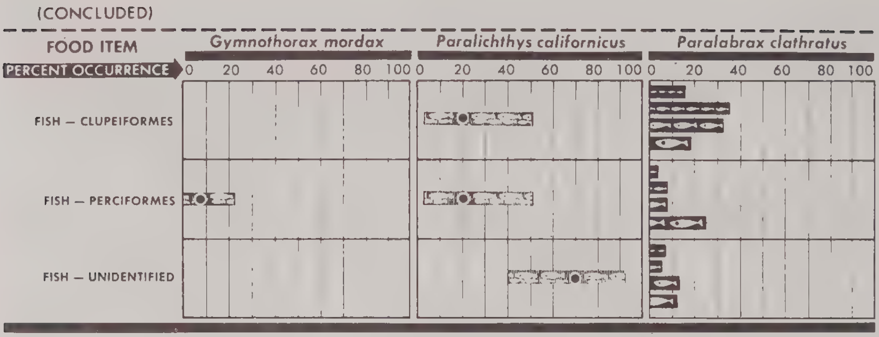


FIGURE 35. Food of California moray, California halibut, and kelp bass. Confidence intervals not presented for the kelp bass because of the large number of specimens.

to larger, more motile prey, such as fishes and cephalopods. Contrary to the implications in its accepted common name, the species normally occurs in habitats with physical relief in any form, whether or not kelp is present.

Sand Bass, *Paralabrax nebulifer* (Figure 36)

The specimens used, representing all seasons, nearly all came from sportfishing boats in or near kelp beds. Depth of capture was 30 to 60 feet.

Sand bass are more demersal than kelp bass; all sightings were within several feet of the bottom. They were noted in greatest abundance near the "edge" habitats, where rocky and sandy areas meet. Shrimp, crabs, ophiuroids, and fish were principal foods. Shrimp occurred in variety, but pistol shrimp were rare. Crabs were mainly spider and cancroid types; the pelagic red crab, *Pleuroncodes planipes,* was relatively infrequent. Nearly all ophiuroids were *Ophiothrix spiculata,* a common form. Probably fish were an important prey, but the data were badly biased toward clupeiform entries by the collection methods. Perciform fishes included *Artedius* sp., *Runula* sp., and unidentifiable fragments. Limbaugh (*l.c.*) noted "squid, small fish, and (once) the eggs of the tubenose (*Aulorhynchus flavidus*)."

Topsmelt, *Atherinops affinis* (Figure 36)

Specimens in the smaller size-group were seined from schools in large rocky tide pools during March and April 1960; fishes in the larger group were speared about kelp and rock-and-sand habitats during all seasons. Adults school and typically feed within 10 to 15 feet of the surface over shallow rocky areas or in kelp beds. Schools were common about clearings in the beds and also in the lee of isolated kelp-plant canopies when winds developed surface currents.

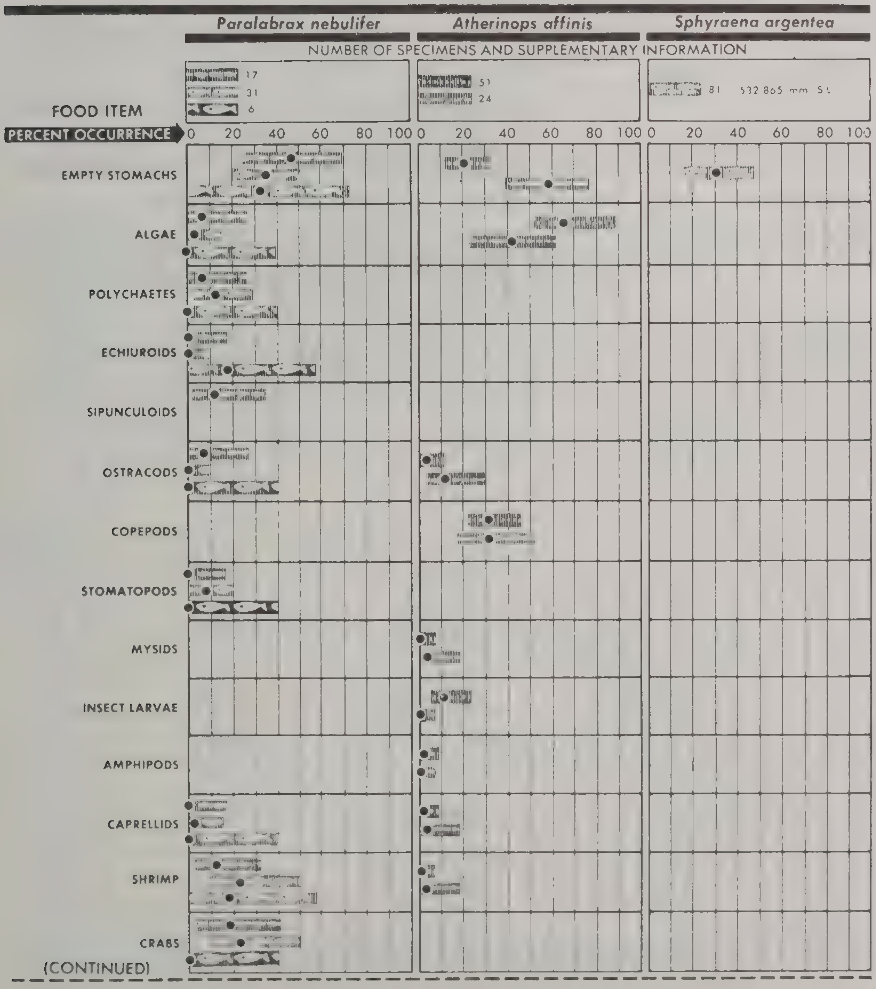
Minute planktonic Crustacea were the principal adult foods. Bryozoans indicated were pelagic larvae. Juveniles and small adults from tide pools contained quantities of small algae and fly larvae (presumably from a kelp fly, noted in great numbers about the splash zone). Limbaugh (*l.c.*) concluded that topsmelt "feed on the many small crustaceans that live in the [kelp] canopy, as well as the planktonic forms that drift into the kelp."

California Barracuda, *Sphyraena argentea* (Figure 36)

This species occurs only incidentally in kelp beds. Specimens used were taken from sportfishing boats adjacent to kelp beds in August 1958. Food was entirely fish, principally anchovies (used as bait and "chum" by the sportfishing boats). Perciform items included señorita (*Oxyjulis californica*) and a juvenile queenfish, *Seriphus politus*. In addition to fish, Limbaugh (*l.c.*) found squid in their diet, and Fitch (*l.c.*) listed anchovies and other small pelagic fishes.

Sargo, *Anisotremus davidsoni* (Figure 37)

Nine of 11 specimens used measured 100 to 199 mm; all but one were taken from rock-and-sand habitats. Specimens were speared during all seasons. Principal foods were small isopods, amphipods, shrimp, and kelp scallops, *Pecten latiauratus*. Limbaugh (*l.c.*) reported "small crustaceans and mollusks, including clams and a chiton."



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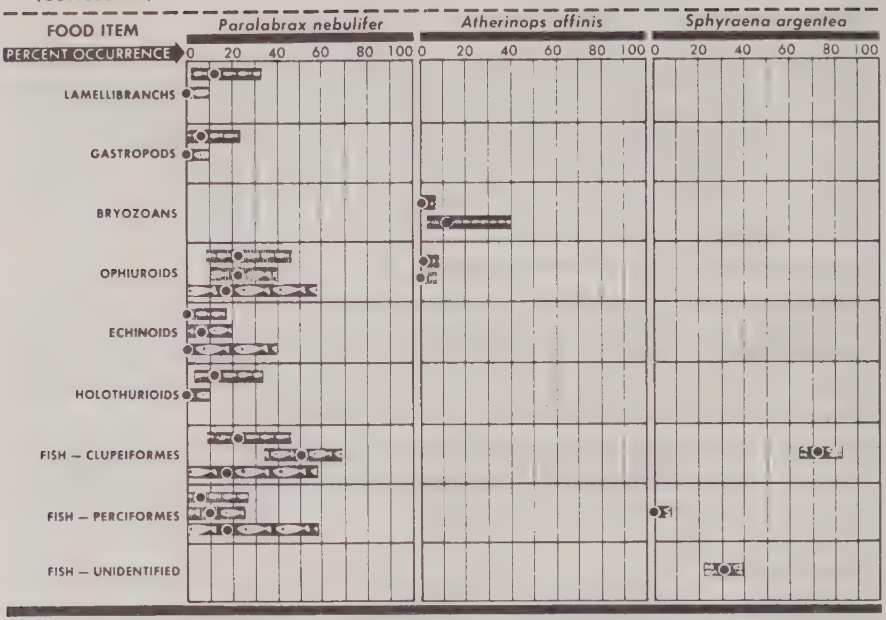


FIGURE 36. Food of the sand bass, topsmelt, and California barracuda.

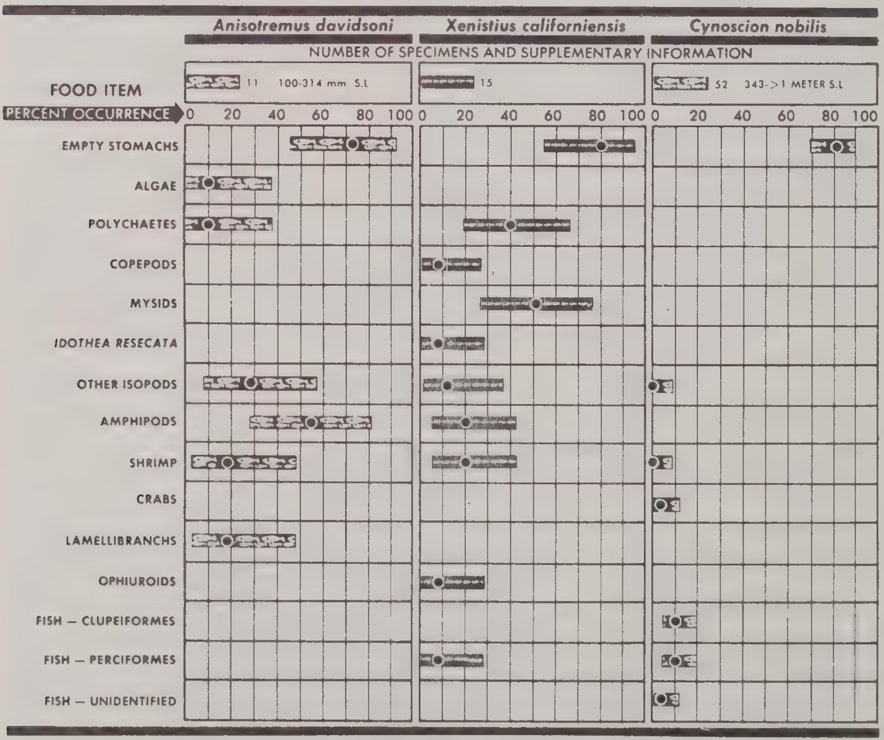


FIGURE 37. Food of the sargo, salema, and white seabass.

Salema, *Xenistius californiensis* (Figure 37)

Entire sample, poisoned by rotenone in July 1959, was from a young kelp bed 25 feet deep, with mixed sand-and-rock substrate. The food data were of questionable validity because of the collecting methods. Mysids and polychaetes, common about kelp fronds, may have become unusually available due to poisoning before the fish succumbed. The bottom-inhabiting ophiuroids, however, probably were ingested prior to the collection.

White Seabass, *Cynoscion nobilis* (Figure 37)

Although many specimens were obtained from sportfishing boats using anchovies for "chum" and bait during summer and winter, the food data are few, because empty stomachs were unusually frequent. Probably the bait was not swallowed by the specimens and was lost before they were brought aboard. Limbaugh (*l.c.*) reported "squid and small fish, such as anchovies and sardines" from their stomachs. Fitch (*l.c.*) reported that some large individuals had fed exclusively on Pacific mackerel (*Scomber japonicus diego*).

Black Croaker, *Cheilotrema saturnum* (Figure 38)

Specimens used were collected during summer and fall in water shallower than 30 feet; three were obtained by rotenone, the remainder by spear. Bottom-dwelling crustaceans were indicated as a principal food in the small sample. Kelp isopods (*Idothea resecata*) were from poisoned fish and may not be representative. Limbaugh (1961) concluded from an intensive study that individuals

> "feed exclusively on crustaceans, and mainly on rock-dwelling crabs, such as the lumpy crab, *Paraxantheas taylori* Stimpson and young moss-covered crabs, *Loxorhynchus crispatus* Stimpson. The lumpy crab seems to be favored. Red-and-white shrimp, *Hippolysmata californica* Stimpson and various amphipods are also consumed. In general, the black croaker is nocturnal in its feeding and other behavior."

Skogsberg (1939) "guessed" a broader diet for the species, and was supported by our findings, which included fish remains, polychaetes, and algae.

A juvenile specimen held in an aquarium for 6 months with a similar-sized kelp bass retained its juvenile pattern of horizontal black stripes until it died from unexplained causes at a total length of 130 mm. Its high activity during the day contrasted with the cryptic diurnal habits of the dark-colored adults. It successfully established a territory that encompassed about two-thirds of the sand bottom. Threat behavior against the kelp bass was frequent and consisted of swimming with the body axis inclined head downward (20–30° from horizontal) back and forth in front of the other fish. During threat activity swimming motions became noticeably "tighter" and more abrupt. "Tail slapping" and sidewise rocking of the body about a vertical axis preceded actual physical combat. Usually, the light areas of the croaker darkened during threat activity and after actual combat the juvenile usually became very dark and closely approximated the adult pattern.

Before the juvenile croaker took food items into the mouth, they were nearly always touched by the chin and (presumed) sensory elements. Considerable daytime activity was devoted to swimming slowly over the sand with the chin approximating or actually in contact with the bottom. In this fashion, the fish located and expertly extracted small sand crabs (*Emerita analoga*) from the sandy substrate. The fish also used the sensory structures on the chin to orient itself to an empty cockle shell on the bottom, prior to rubbing its sides against the shell.

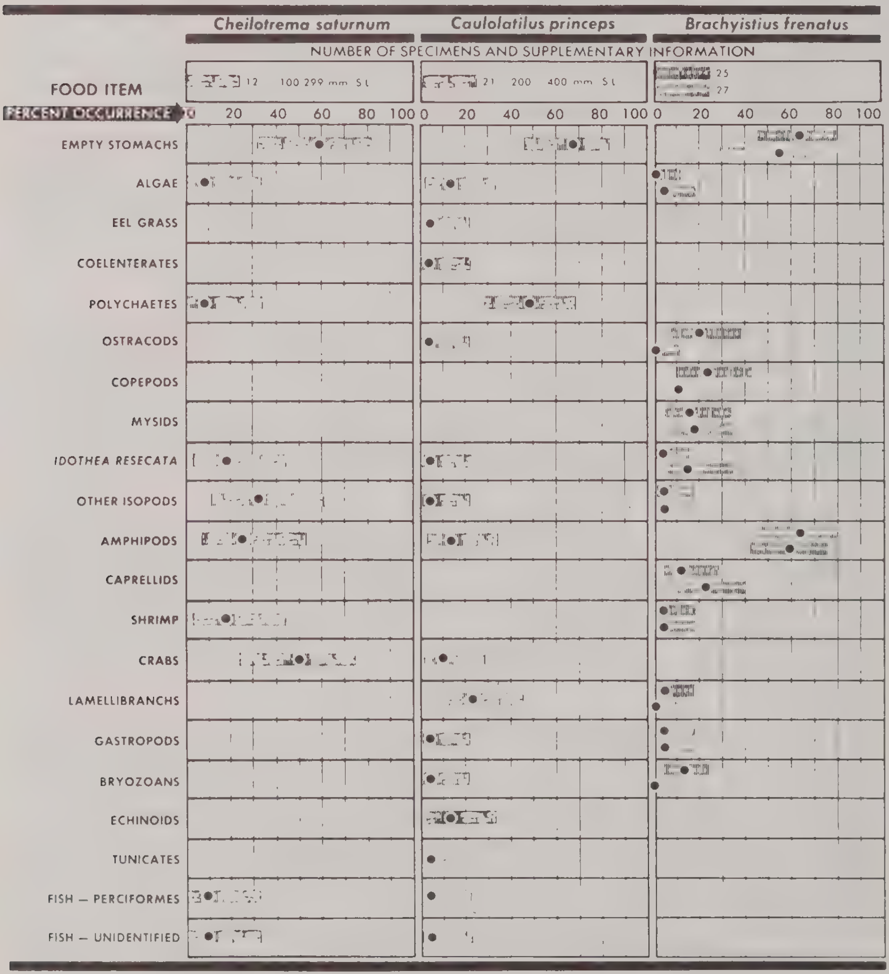


FIGURE 38. Food of the black croaker, ocean whitefish, and kelp perch.

Ocean Whitefish, *Caulolatilus princeps* (Figure 38)

Specimens used, all but three from kelp-bed habitats, were speared during winter at depths of 30 to 110 feet. Four-fifths were between 300 to 500 mm SL. All items indicated bottom-feeding habits; tube-dwelling polychaetes were the principal food. Lamellibranch entries included razor clams, kelp-scallop shells, and small clams. Fitch (*l.c.*) noted they "eat just about anything they are capable of getting their mouths around—especially crabs, shrimp, and other crustaceans,'' and that small octopuses, squid, and assorted fish also enter the diet.

Kelp Perch, *Brachyistius frenatus* (Figure 38)

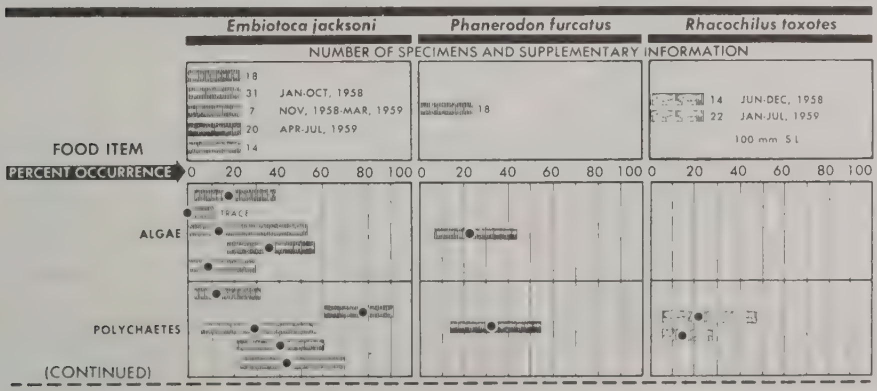
This fish is usually abundant in and about the kelp columns and canopy, and nearly all specimens used were obtained by rotenone from kelp beds, during summer, winter, and fall. The natural food probably resembles that found in the poisoned fish, and small crustacea associated with kelp plants are heavily utilized. Limbaugh (*l.c.*) stressed that the kelp perch is an important parasite picker on other fishes but limited observations in this study did not reveal such behavior. No external parasites were identified in the digestive tracts.

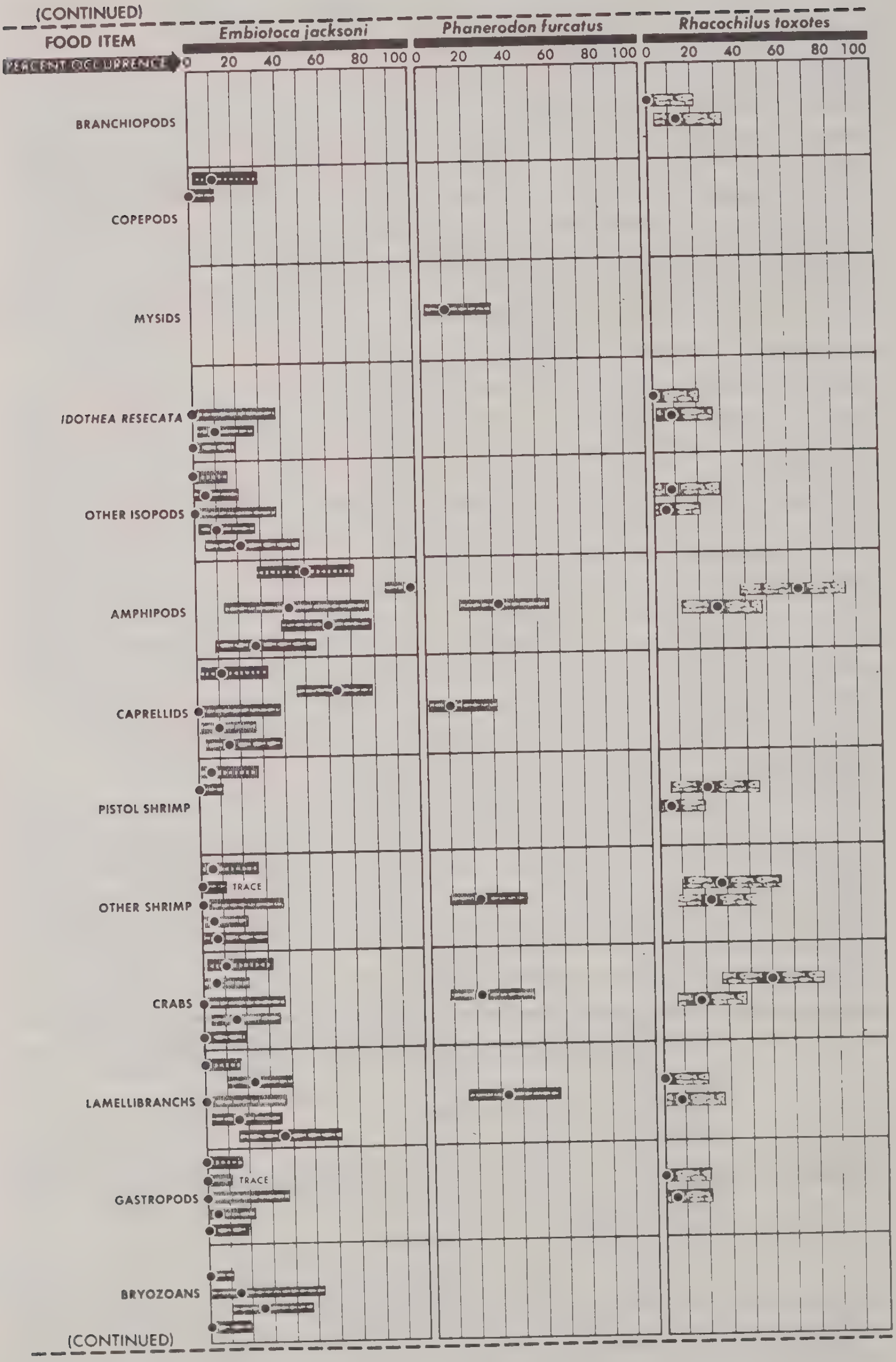
Black Perch, *Embiotoca jacksoni* (Figure 39)

Approximately equal numbers were collected by spear and by rotenone. Individuals were typically seen roaming the bottom (the adults singly or in loosely associated groups of three to five), nearly always in association with tufted algae of rocky areas, from which they undoubtedly obtain their food. Principal foods were polychaete worms, gammarid amphipods, caprellids, and spider crabs, all of which abound in the tufted-algae habitat. Small amounts of algae noted undoubtedly were taken incidental to the capture of invertebrates. *Lima,* small *Mytilus,* and small *Pecten,* frequently taken entire, composed the lamellibranch entries. Limbaugh (*l.c.*) found ''crustaceans, mollusks, bryozoans, and worms,'' in the black perch and also mentioned the presence of external parasitic fish crustaceans in their diets, but none were noted in the stomach contents of the specimens we examined.

White Seaperch, *Phanerodon furcatus* (Figure 39)

Data were from a single sample collected by rotenone in June 1958 from a kelp bed near Del Mar, California. Principal foods were bottom-dwelling small crustaceans, polychaetes, and bivalves. Numerous *Macrocystis* fragments were noted, some heavily encrusted by bryozoans. Crustacean entries included crabs, shrimp, caprellids, mysids, and assorted gammarid amphipods (many were elongate and had large chelae). Some polychaetes were enclosed by sand-encrusted tubes. La-




(CONTINUED)
FOOD ITEM
PERCENT OCCURRENCE
Embiotoca jacksoni
Phanerodon furcatus
Rhacochilus toxotes
0
20
40
60
80
100
BRANCHIOPODS
COPEPODS
MYSIDS
IDOTHEA RESECATA
OTHER ISOPODS
AMPHIPODS
CAPRELLIDS
PISTOL SHRIMP
OTHER SHRIMP
TRACE
CRABS
LAMELLIBRANCHS
GASTROPODS
TRACE
BRYOZOANS
(CONTINUED)

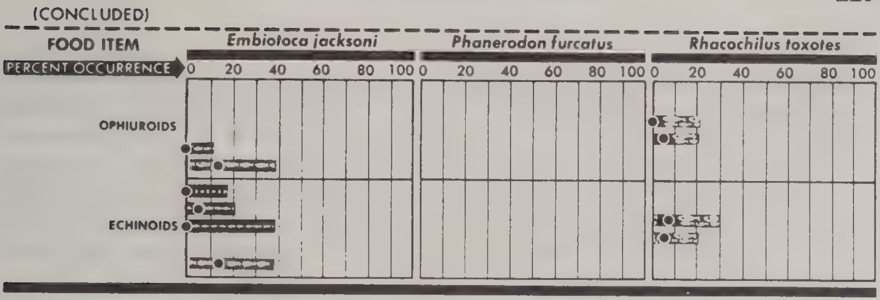


FIGURE 39. Food of the black seaperch, white seaperch, and rubberlip seaperch.

mellibranchs included small mussels, taken entire, and kelp-scallop shells.

Because the data were based on a single poison collection, there is some doubt concerning reliability. Mysids, caprellids, and numerous small gammarid amphipods normally are present in the kelp canopy and may have become unusually available during the poisoning. The kelp fragments may have originated from outboard motors operated in the area prior to actual collection.

Rubberlip Seaperch, *Rhacochilus toxotes* (Figure 39)

Twelve specimens were taken by rotenone at the Del Mar kelp bed, the remainder were collected by spear. Food was very similar in rotenoned and speared specimens; small shrimp and gammarid amphipods were utilized heavily. Small crabs also were frequent. Two adult fish (300 mm SL) had fed nearly exclusively on marine branchiopods (*Nebalia* sp.). One 197-mm specimen contained late megalops crab larvae. Among other bottom-dwelling crustacea were a stomatopod (not depicted in the figure) and numerous pistol shrimp.

Pile Perch, *Rhacochilus vacca* (Figure 40)

Two-thirds were from rotenone collections, the rest was collected by spear. All seasons are represented. Demersal shelled invertebrates, principally hermit crabs, were very important in all samples. Lamellibranchs included small forms, such as *Chione, Donax,* and small *Mytilus.* Gastropod frequencies apply mainly to crushed snail shells mixed with remains of the former hermit crab inhabitants.

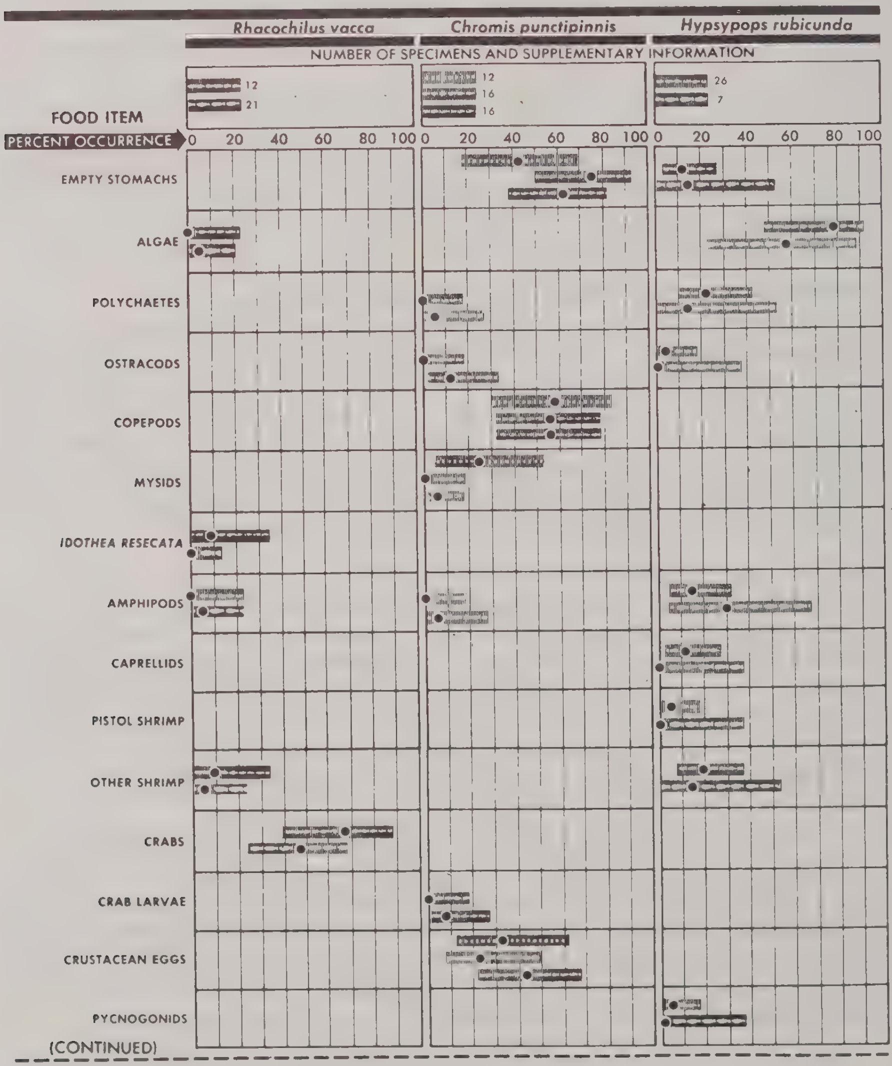
Limbaugh *(l.c.)* also studied this species and came to slightly different conclusions regarding its diet. He stated,

> "They feed on clams (such as mussels and bean clams), gastropods (including limpets, dove shells, cones, and smooth tops), chitons, decapods, other crustaceans, ophiuroids, and sand dollars. They are commonly observed around pilings pulling small mussels free, crushing them in their throats as they swallow them. A half-grown specimen was observed being forced into eating external fish parasites by a group of blacksmith."

Probably Limbaugh's collections were taken principally from shallow water near Scripps in sand-and-rock or sand-and-pier-piling habitats, where this species sometimes abounds. Available food in these regions differs considerably from that at 30-80 feet in kelp beds.

Blacksmith, *Chromis punctipinnis* (Figure 40)

Seventeen specimens were taken by rotenone, the remainder speared. All seasons are represented. Principal foods are minute swimming crustacea and crustacean eggs and larvae gleaned from open-water spaces in kelp beds and over rocky areas. The topsmelt, with a similar diet, feeds in the surface regions normally above the zone of the blacksmith, although the two feeding levels may overlap. Limbaugh (1955) noted that blacksmith feed on ''particulate plankton such as small fish, squid and crustaceans.''



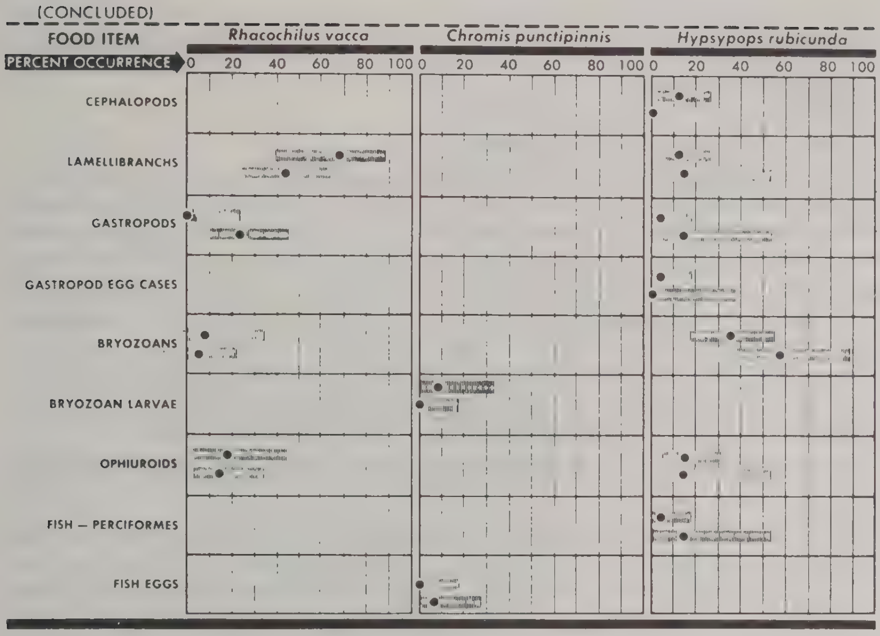


FIGURE 40. Food of the pile perch, blacksmith, and garibaldi.

Garibaldi, *Hypsypops rubicunda* (Figure 40)

Approximately one-third of the specimens used were spear-collected, the rest obtained by rotenone. Spring and summer are represented. Small flabellate and coralline red algae, brown and green algae, and upright bryozoans were the principal items. Polychaetes, shrimp lamellibranchs, gastropods, ophiuroids, and fish also were found. Shrimp entries were mainly the red rock shrimp *Hippolysmata californica*; these as well as the fish were obtained exclusively in the rotenone collections and may not represent the normal diet. Correct interpretation of the data is difficult because the male builds and guards a nest on a flat rock surface in the summer. All but a velvet-like red algae are removed and presumably eaten. However, algae were in the stomachs of both sexes and its presence therefore was not the sole result of nest construction and maintenance.

Limbaugh *(l.c.)* studied the breeding and food of the garibaldi and concluded that they "probably prefer bryozoans to other organisms. Other organisms found in their stomachs include sea anemones, worms, tiny crustaceans (crabs, shrimps, etc), clams, snail eggs, gooseneck barnacles, and even eggs of their own species." The data from both investigations indicate that the garibaldi probably is omnivorous. Although browsing short algae from rocks may contribute some nourishment, the entrapped invertebrates attached to the plants undoubtedly contribute substantially to nutrition.

Rock Wrasse, *Halichoeres semicinctus* (Figure 41)

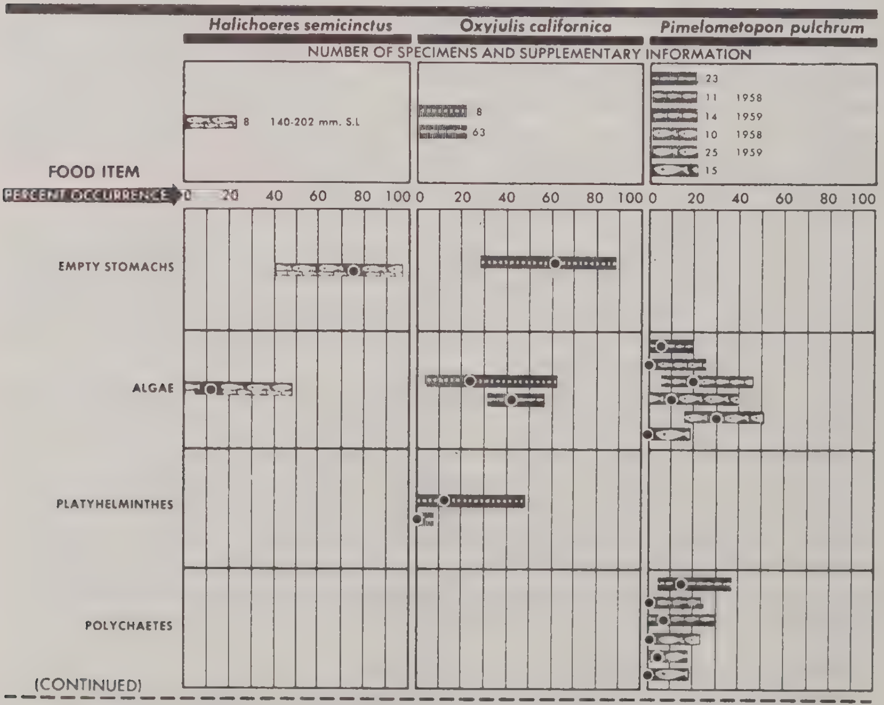
All specimens were collected from 25 to 35 feet deep, all but one by spear. Winter and summer are represented. Foods included algae, spider crabs, kelp scallops, dove snails, bryozoans, and the common serpent star, *Ophiothrix spiculata*. Because so few specimens were obtained, the analysis may not be highly representative. Limbaugh *(l.c.)* listed amphipods, small decapods, dove shells, and one slipper shell in the diet.

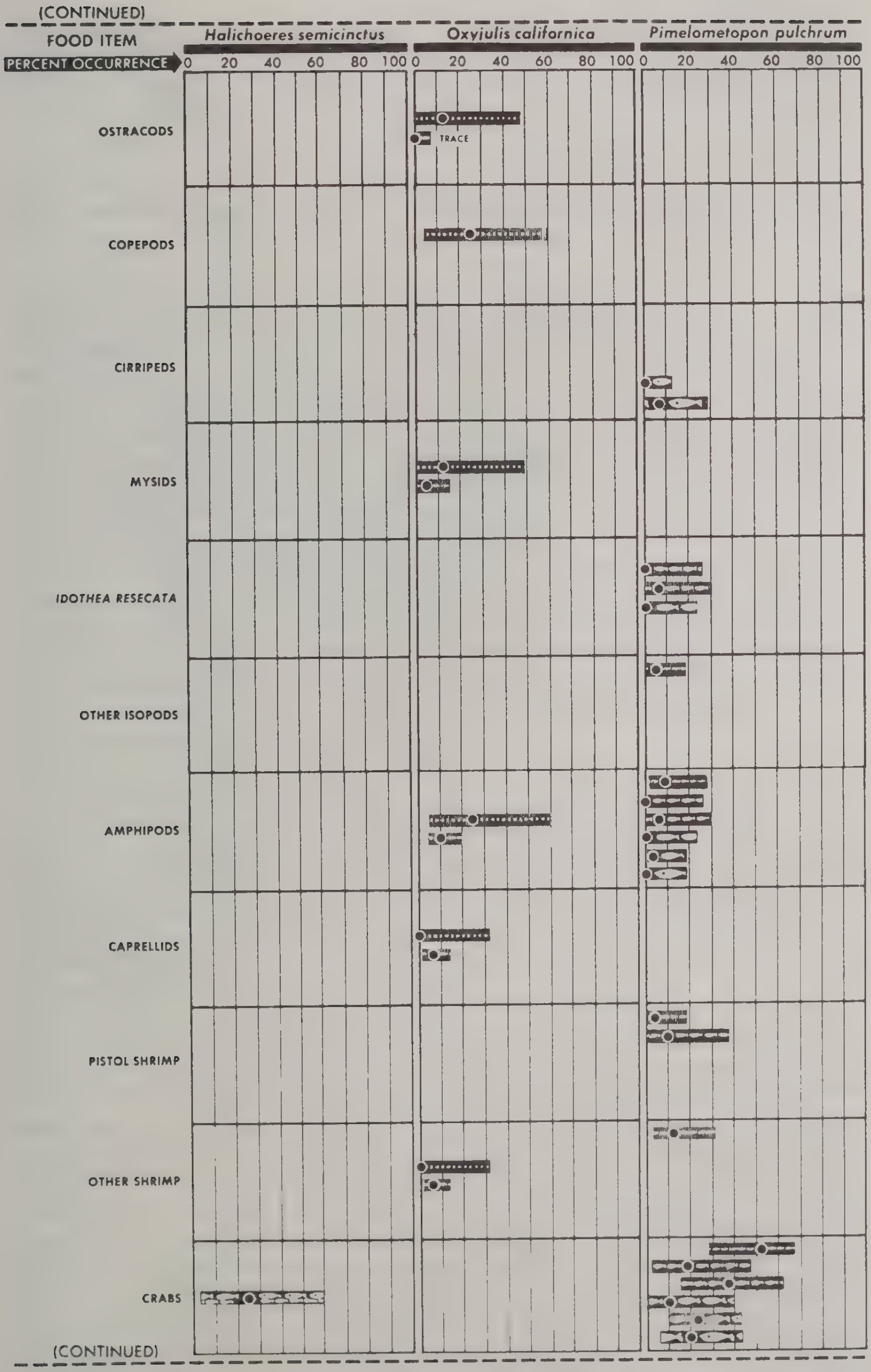
Señorita, *Oxyjulis californica* (Figure 41)

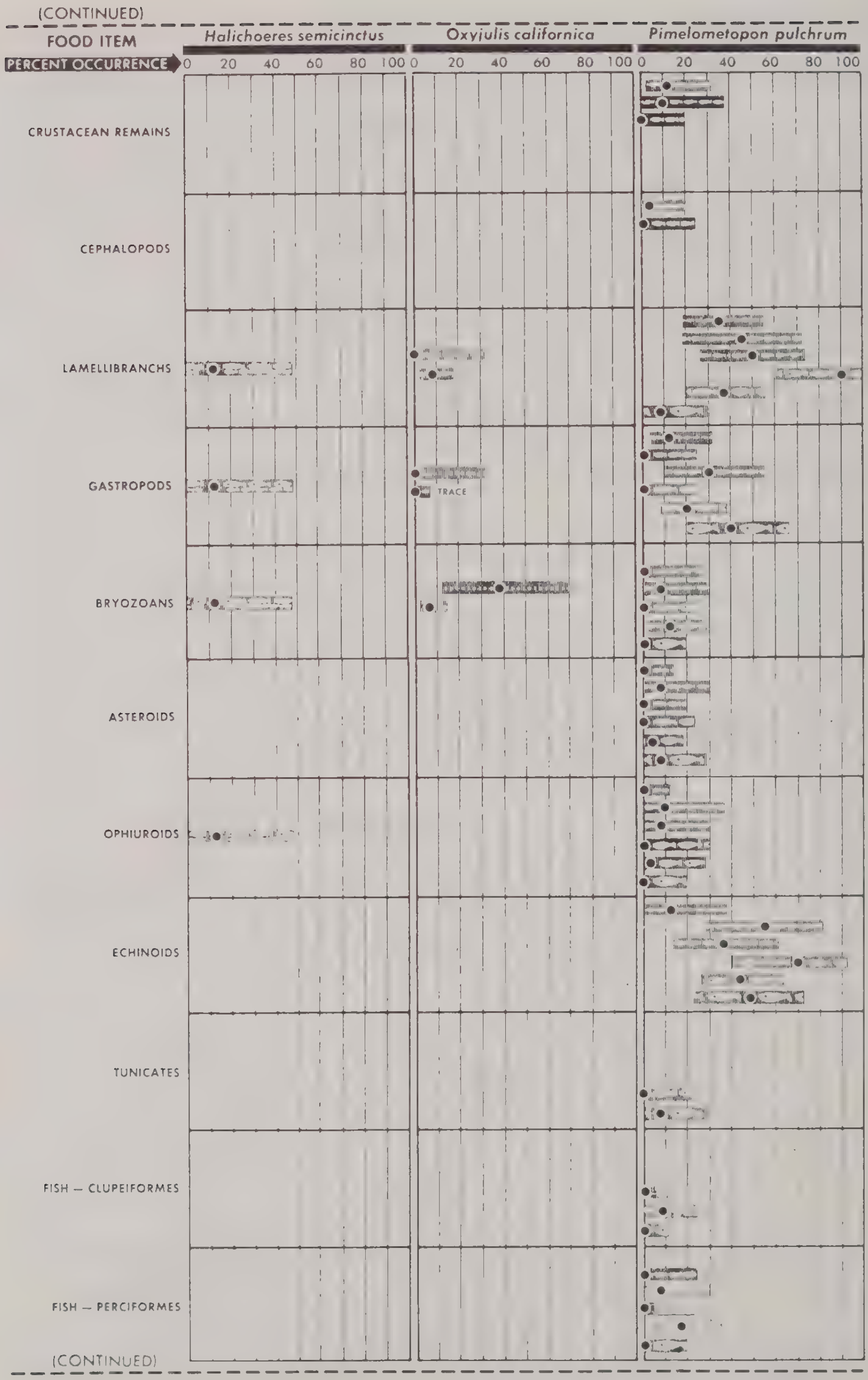
Approximately equal numbers were taken by spear and by rotenone. All seasons are represented. Principal foods were small gastropods and crustaceans commonly associated with algae. *Macrocystis* fragments were numerous in specimens from the Del Mar collection and may either have been taken incidentally to feeding on attached crustacea and gastropods or swallowed after the kelp was fragmented by outboard motors. The absence of crab and pistol shrimp in all collections suggested that bottom-feeding is infrequent. Small (50 to 60 mm SL) individuals fed heavily on copepods, ostracods, and small triangular bryozoan larvae (measuring approximately 0.3 mm on a side.)

Limbaugh *(l.c.)*, who made extensive notes on the señorita habits and life history, concluded:

> "Señoritas are omnivorous, carnivorous, feeding on almost any animal protein, continually picking at small objects on the bottom, on plants, other fishes, or from the water itself. When plankton is heavy with larval fish, squid, or small crustaceans, large schools of señoritas, along with blacksmith and topsmelt, often intercept the inflowing current in a kelp bed or in a bay entrance."




(CONTINUED)
FOOD ITEM
PERCENT OCCURRENCE
Halichoeres semicinctus
Oxyjulis californica
Pimelometopon pulchrum
0
20
40
60
80
100
OSTRACODS
TRACE
COPEPODS
CIRRIPEDS
MYSIDS
IDOTHEA RESECATA
OTHER ISOPODS
AMPHIPODS
CAPRELLIDS
PISTOL SHRIMP
OTHER SHRIMP
CRABS
(CONTINUED)


(CONTINUED)
FOOD ITEM
PERCENT OCCURRENCE
Halichoeres semicinctus
Oxyjulis californica
Pimelometopon pulchrum
0 20 40 60 80 100
CRUSTACEAN REMAINS
CEPHALOPODS
LAMELLIBRANCHS
GASTROPODS
TRACE
BRYOZOANS
ASTEROIDS
OPHIUROIDS
ECHINOIDS
TUNICATES
FISH — CLUPEIFORMES
FISH — PERCIFORMES
(CONTINUED)

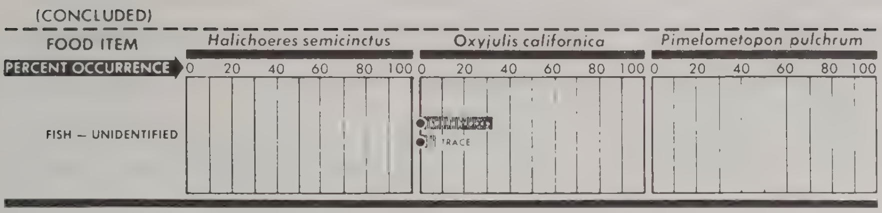


FIGURE 41. Food of the rock wrasse, señorita, and California sheephead.

California Sheephead, *Pimelometopon pulchrum* (Figure 41)

Specimens were taken principally from rocky-bottom habitats near kelp, at depths of 30 to 80 feet, nearly all by spear, a few by hook and line. All seasons are represented. Principal foods were fixed and slow-moving bottom invertebrates, such as tube-dwelling polychaetes, crabs, lamellibranchs, gastropods, and echinoids. Algae probably were taken incidentally to capture of small crabs and gastropods. Hermit crabs and *Pleuroncodes* occurred. Lamellibranchs included an abundance of kelp scallops, which were probably eaten entire and were common on the kelp during the studies. Other mollusks were *Lima, Olivella, Mitrella,* and turban snails (the turban-snail entries frequently coincided with hermit crabs.) High percentages for echinoids were due in part to baiting with crushed sea-urchins when fish were spear-collected. High sea-urchin frequencies for hook-and-line specimens may have been caused in part by sportfishing boats dragging their anchors and chains somewhat when fishing, thus undoubtedly crushing many sea-urchins on the bottom.

Limbaugh (1955) noted:

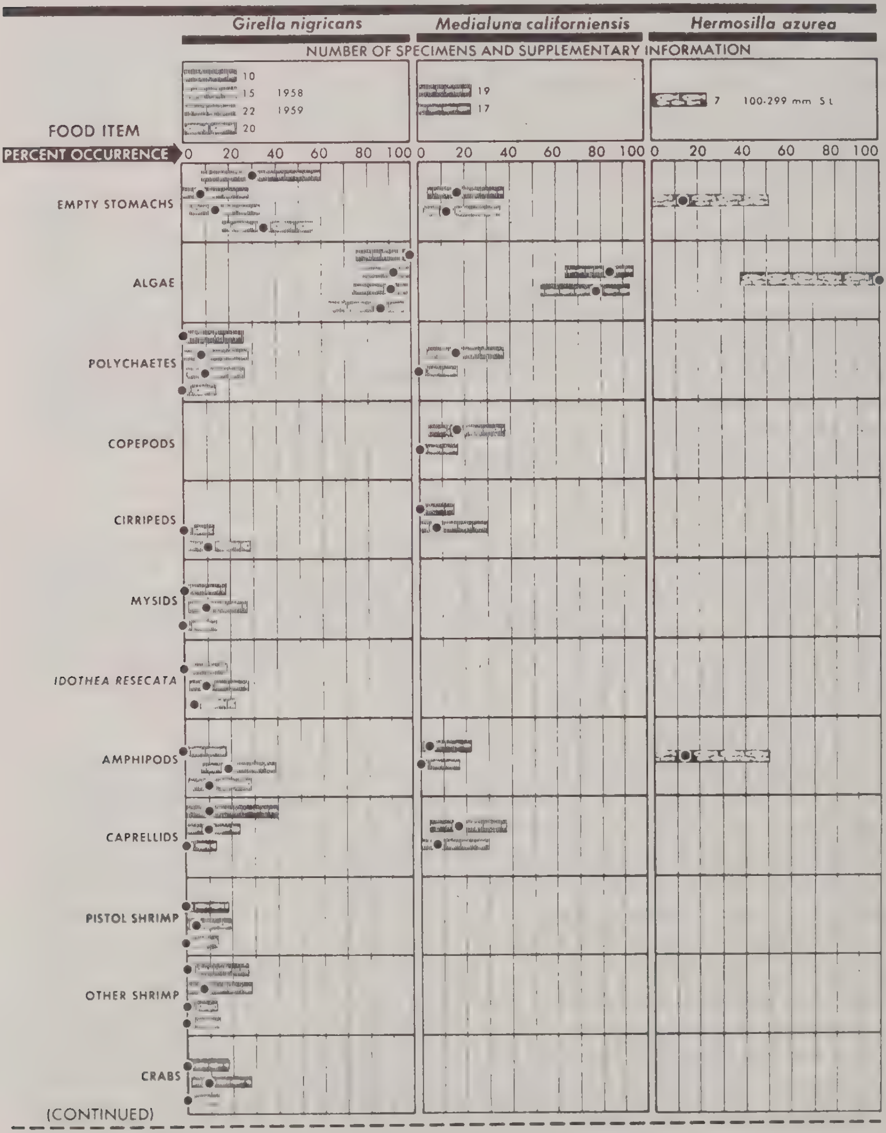
> "the adults feed on sea urchins, mussels, crabs, large and small snails, squid, bryozoans, sand dollars, and sea cucumbers. They crush the food in their throats as they swallow it. On several occasions large adults were observed above water hanging onto mussels after a wave had retreated. Those found around mussel beds seem to attain the largest size."

Opaleye, *Girella nigricans* (Figure 42)

Seven specimens were collected with rotenone, nearly all others by spear. All seasons are represented. Depths of collection were 30 to 80 feet. Even in fish with empty stomachs, the intestines were nearly always packed with algae (fleshy and coralline reds, as well as green and brown types). Flattened and filamentous reds predominated in occurrence and volume; next in frequency were flattened and filamentous greens. Although *Macrocystis* and coralline algae appeared in approximately equal frequencies, individuals containing *Macrocystis* usually had their digestive tracts packed with that kelp. Brown algae other than *Macrocystis* were least frequent. Some eelgrass (*Phyllospadix*) was also noted. Limbaugh (*l.c.*) noted ribbon kelp, giant kelp, sea lettuce, *Gelidium*, coralline algae, bryozoans, and sinistral worms.

Williams and Williams (1955) concluded that 23-to-32 mm young have a mixed plant-animal diet but that larger fish are primarily herbivorous because plant materials predominate in their digestive tracts.

However, both Williams and Williams (*l.c.*) and Limbaugh (*l.c.*) recognized that animal materials in the forage may be the principal source of nutrition for both young and adults despite the large bulk of algae. Several observations during the Kelp Program studies support this conclusion. Twelve small-adult opaleye, for example, were held in a large aquarium and restricted to a diet of clean *Macrocystis*. They failed to gain weight and died in approximately 1 month while single specimens held in similar aquaria thrived on diets of trout pellets or crustaceans. No alginase activity was evident in the gut of a fresh healthy adult specimen collected by spear (Reuben Lasker, personal



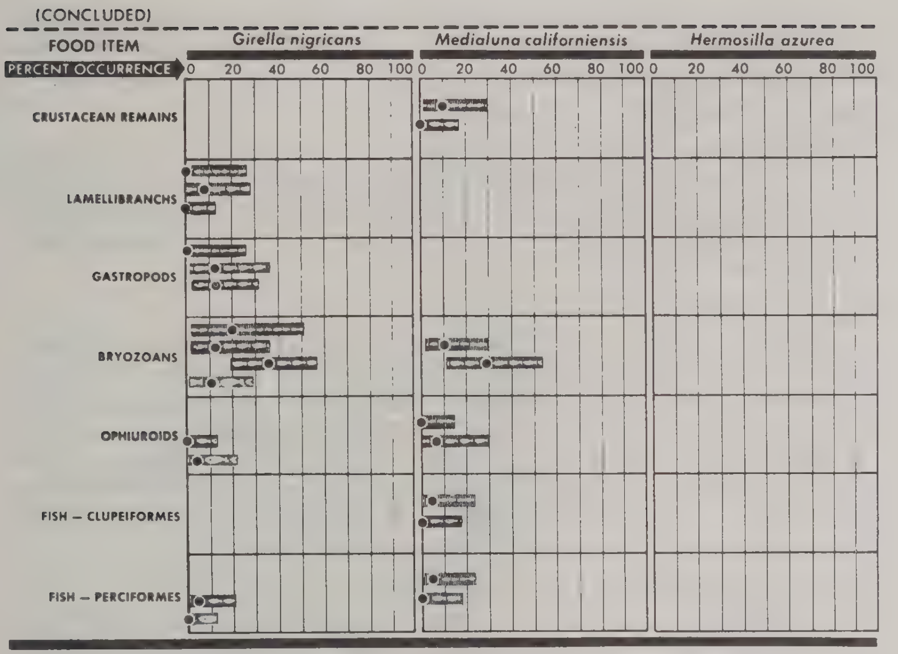


FIGURE 42. Food of the opaleye, California halfmoon, and zebraperch.

communication), although similar methods gave strong positive results for the sea-urchin, *Strongylocentrotus purpuratus* (Eppley and Lasker, 1959).

Norris and Prescott (1959) concluded that the teeth of the opaleye probably are "a complex structural adaptation to a grazing or scraping type of food-getting," and that "the structures combine to allow individual teeth to move closely over the inequalities of rock surfaces as the animal scrapes loose encrusting algal scums or fine filamentous algae." I have observed that opaleye use a very different method while feeding on tufted algae and *Macrocystis*. While the alga is held in the mouth portions are severed by a strong sidewise motion of the head and body. Characteristic circular sections are removed from *Macrocystis* fronds in this fashion. Probably the alga is severed by the sawlike action of the teeth as the head is moved laterally.

Halfmoon, *Medialuna californiensis* (Figure 42)

Six specimens were collected by rotenone, the remainder by spear. All seasons are represented. Depths of capture ranged from 30 to 80 feet. Like the opaleye, this species was common about rocky inshore areas and kelp beds, but was usually much more abundant than opaleye in deeper beds, especially those at considerable distances offshore and about islands. The food resembled that of the opaleye and included a large variety of algae. Animals may also furnish the principal nutrition in this species. However, Follett, Gotshall, and Smith (1960) noted that some aquarium-held specimens apparently declined in condition after approximately 6 months on animal food, but returned to good health by feeding on algae, principally *Macrocystis* and *Egregia*. Limbaugh (*l.c.*) found red, green, and brown algae in their diet, as well as bryozoans and sponges.

Zebra Perch, *Hermosilla azurea* (Figure 42)

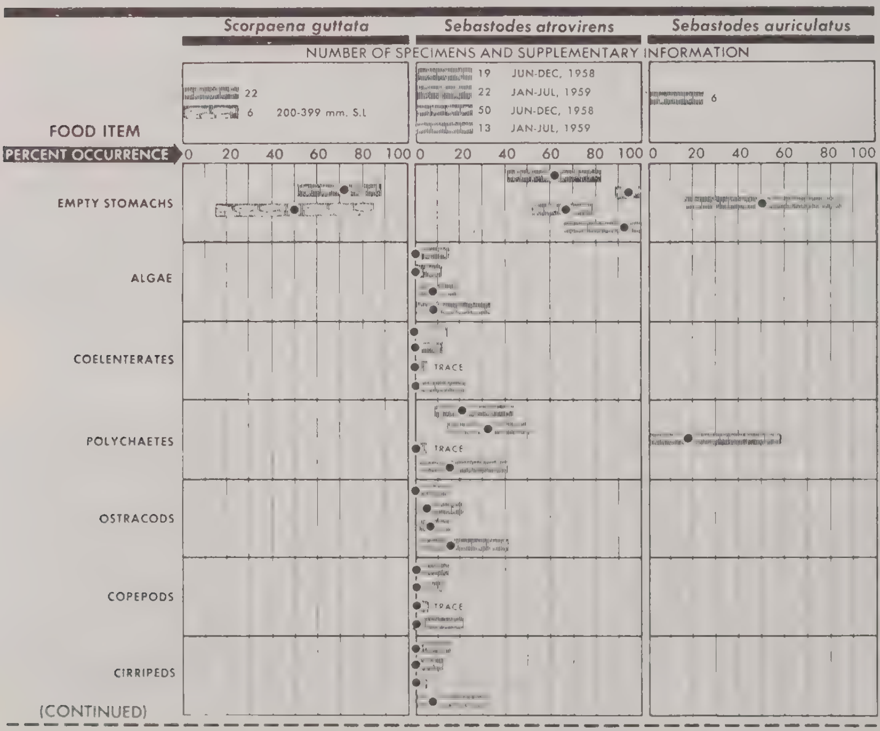
All specimens used were taken by spear; collections were scattered throughout the year. Individuals were seen only in shallow, warm waters near shore. Stomach contents resembled those of opaleye and halfmoon and principal nutrition probably was gained from animal material consumed with algae.

Sculpin, *Scorpaena guttata* (Figure 43)

Over three-fourths were taken by rotenone from kelp areas. All seasons are represented. Depths of capture ranged from 25 to 35 feet. Foods from 100 to 199 mm fish were mainly demersal crustaceans such as crabs, shrimp, and caprellids. Some squid and fish occurred. Fish and cephalopods increased in importance in the larger sizes. Adults take an artificial lure near the bottom, and once one grabbed the gloved hand of my diving partner. Limbaugh (*l.c.*) noted crabs, shrimp, octopus, and squid in their diet.

Kelp Rockfish, *Sebastodes atrovirens* (Figure 43)

The majority were taken by spear, the rest by rotenone and hook-and-line. All seasons are represented. Nearly all were from kelp beds at depths of 30 to 80 feet. Individuals ranged from the bottom to the kelp-bed canopy (visual notes), and apparently utilized all available



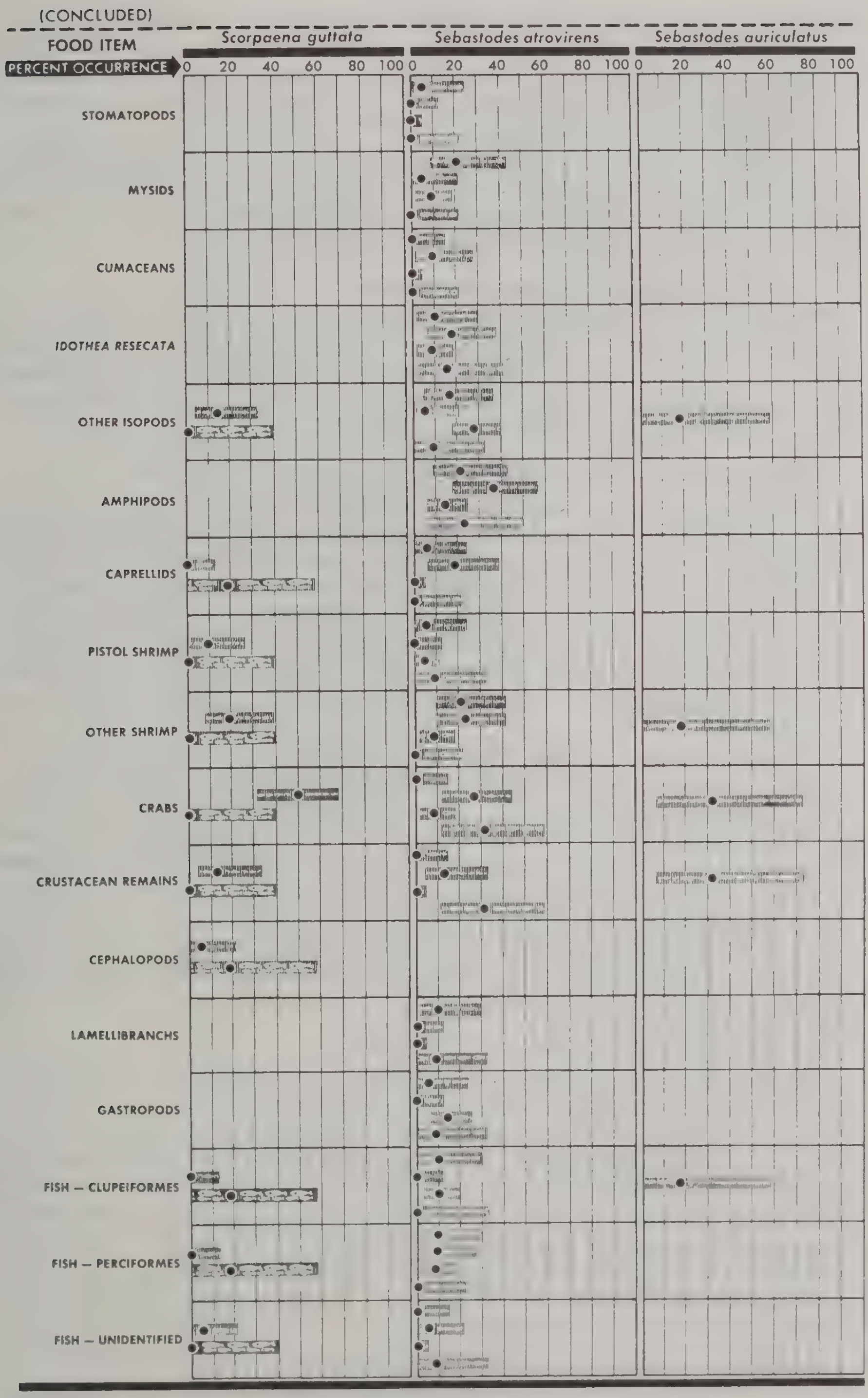


FIGURE 43. Food of the sculpin, kelp rockfish, and brown rockfish.

foods in these regions. Diets of size-groups were similar, except possibly for "other shrimp." Possible seasonal differences in diet were indicated for polychaetes, mysids, *Idothea resecata,* other isopods, gammarid amphipods, caprellids, crabs, gastropods, and clupeiform fish. Limbaugh (*l.c.*) noted "crustaceans and small fish" as their food.

During the Kelp Program studies, individuals noted in the field appeared to be quite thin. Such an appearance may be normal for this species, but the high frequencies of empty stomachs and the broad variety of food items found may indicate malnutrition.

Brown Rockfish, *Sebastodes auriculatus* (Figure 43)

Five specimens were collected, between May and July, by hook-and-line from kelp beds at approximately 60 feet. Only crabs, shrimp, isopods, polychaetes, and clupeiform fish were indicated (the clupeiform entries probably from bait or "chum"). Limbaugh (*l.c.*) noted "crabs and small fish" in their diet.

Gopher Rockfish, *Sebastodes carnatus* (Figure 44)

Nearly all specimens used were speared between 30 to 80 feet, usually in kelp beds. All seasons are represented. Phillips (1957) distinguished *S. carnatus* and *S. chrysomelas* principally by color characteristics. Approximately two-thirds of our specimens fitted the description for *S. carnatus* and most of the rest satisfied the description for *S. chrysomelas*, but some were intermediate. Because the two nominal species may only be color variants, and because they frequently occur side by side, all data were lumped under the more common color type, *S. carnatus.*

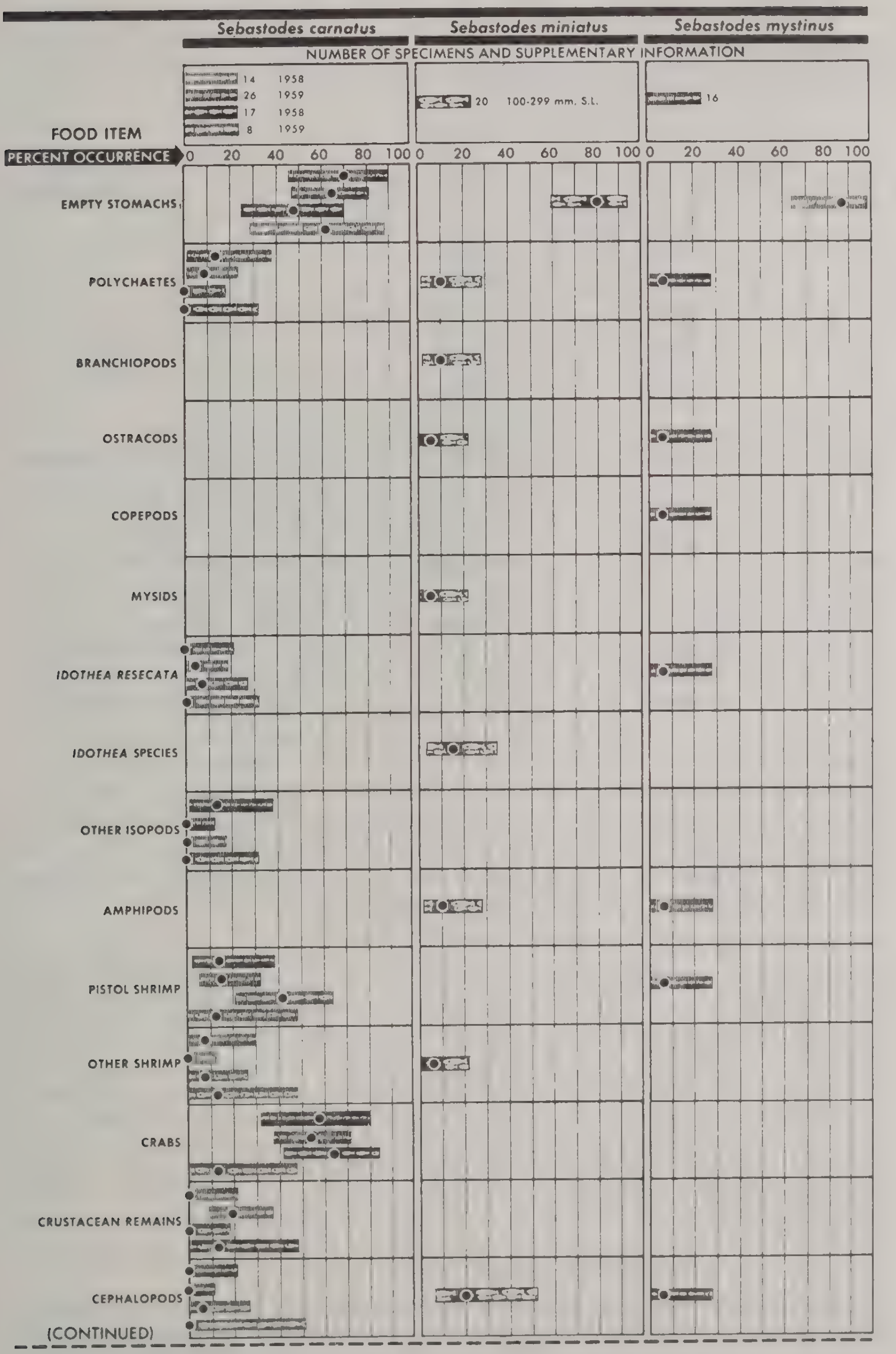
Principal foods were medium-sized crustacea, especially cancroid and spider crabs and pistol shrimp (*Alphaeus dentipes*). Polychaetes, isopods, cephalopods, gastropods, and ophiuroids also occurred. All engraulids came from hook-and-line captures and probably were bait. Perciform entries were mostly small forms such as cottids. Gopher rockfish were relatively fearless and would commonly swim up to a diver, presumably attracted by parts of his attire or the air bubbles. Several times I observed them to swim several feet up from a rocky habitat to tug at a fish on a stringer. Limbaugh (*l.c.*) noted their food as crabs, small fish, and squid.

Vermilion Rockfish, *Sebastodes miniatus* (Figure 44)

Nearly all specimens used were speared at depths of 100 feet or greater, away from kelp beds. All seasons were represented. Although pressure changes when specimens were brought to the surface nearly always caused regurgitation of stomach contents, intestinal material usually yielded useful food information. Squid were quite important and small crustaceans such as mysids were sometimes encountered in considerable volumes (mysids nearly filled the stomach of one small adult). Other foods included *Nebalia,* polychaetes, ostracods, *Idothea,* amphipods, and shrimp. One lancelet, *Branchiostoma* sp., also was noted.

Blue Rockfish, *Sebastodes mystinus* (Figure 44)

Three specimens were obtained by hook-and-line, the remainder were speared. The food data were inadequate because specimens were


Sebastodes carnatus
Sebastodes miniatus
Sebastodes mystinus
NUMBER OF SPECIMENS AND SUPPLEMENTARY INFORMATION
14 1958
26 1959
17 1958
8 1959
20 100-299 mm. S.L.
16
FOOD ITEM
PERCENT OCCURRENCE
0 20 40 60 80 100
EMPTY STOMACHS
POLYCHAETES
BRANCHIOPODS
OSTRACODS
COPEPODS
MYSIDS
IDOTHEA RESECATA
IDOTHEA SPECIES
OTHER ISOPODS
AMPHIPODS
PISTOL SHRIMP
OTHER SHRIMP
CRABS
CRUSTACEAN REMAINS
CEPHALOPODS
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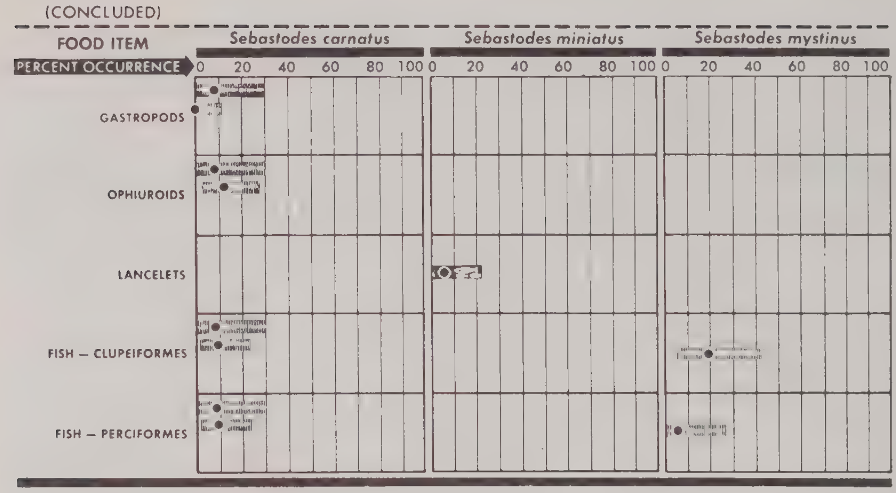

FIGURE 44. Food of the gopher rockfish, vermilion rockfish, and blue rockfish.

few and digestive tracts were frequently empty. Anchovies and, occasionally, small crustaceans were noted. Perciform entries were based on ctenoid scales only.

Individuals swam in large schools that resembled schools of blacksmith, because the species is blue, and, in the San Diego region, of similar size. However, the blue rockfish were not as directly associated with rocky substrate and the fish normally were more widely spaced in the schools. No specimens of breeding size were ever seen and all gonads examined were immature. Visual records were for fish smaller than 200 mm SL and the largest one collected measured 176 mm. All, therefore, were below the size of first maturity given by Wales (1952). As with *S. atrovirens,* the fish appeared to be in poor condition. The blue rockfish may be poorly adapted to the environment of this region and the schools may comprise expatriate populations.

Grass Rockfish, *Sebastodes rastrelliger* (Figure 45)

Collections were obtained at all seasons, from regions shallower than 55 feet and in kelp beds. The species is rare at greater depths. Approximately equal numbers were taken by poison, spear, and hook-and-line. The anchovies that occurred only in hook-and-line specimens probably represented bait. Both cancroid and spider crabs and pistol shrimp were frequent. "Other" shrimp, a *Conus californiensis,* and a small perciform fish (clinid?) also were noted. Limbaugh (*l.c.*) found crabs and small fish in their stomachs, and Baxter (1960) noted a 5-inch white seaperch (*Phanerodon furcatus*) from a 16-inch specimen.

Olive Rockfish, *Sebastodes serranoides* (Figure 45)

Nearly all specimens used were from the kelp-bed habitat. Depths ranged from 30 to 110 feet, and all seasons are represented. Individuals were usually seen off the bottom at about mid-depth. At times they mingle there with kelp bass, which they resemble in form and coloration when alive. Food was similar to that of the kelp bass, and mainly comprised swimming forms and animals associated with

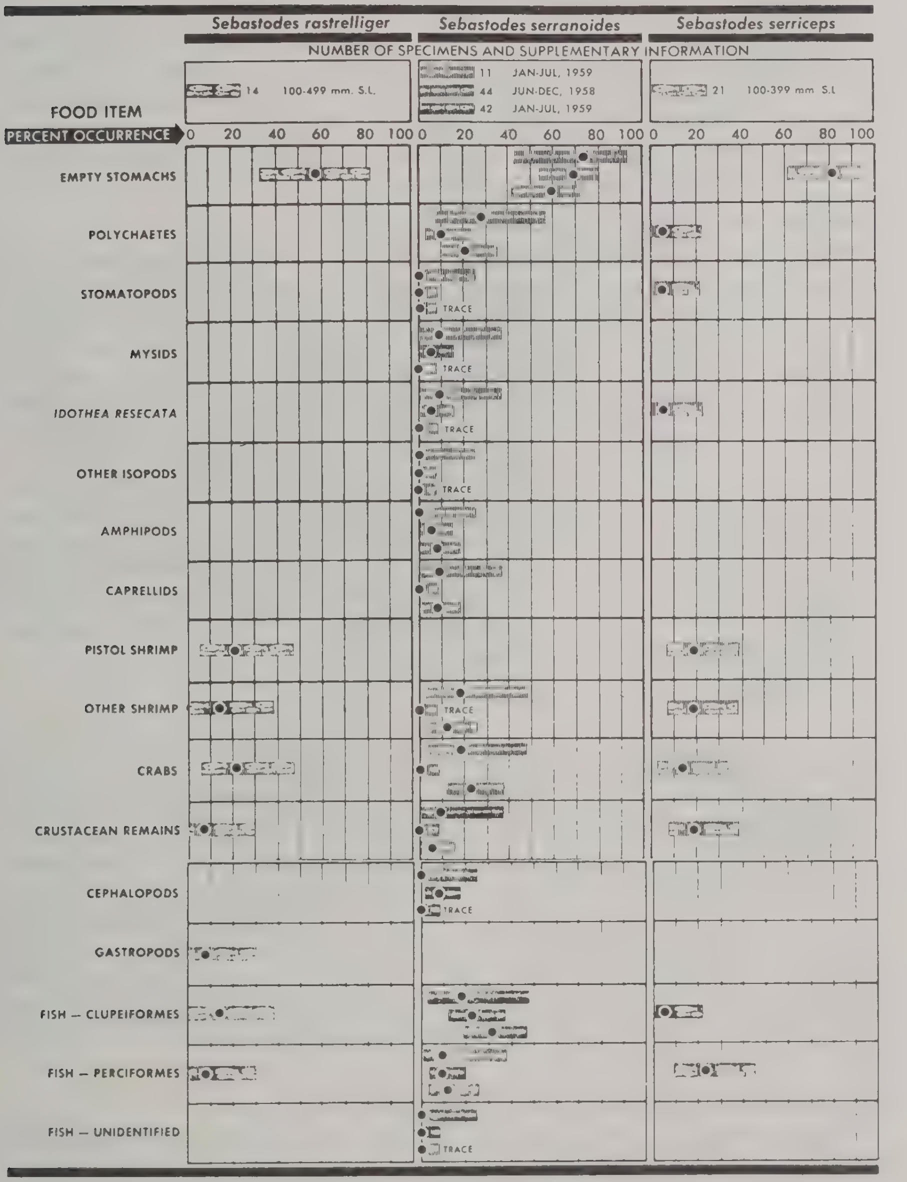

FIGURE 45. Food of the grass rockfish, olive rockfish, and treefish.

the kelp canopy. Crab entries were mainly adult *Pleuroncodes* and megalops larvae. Squid and octopus occurred. Anchovies composed nearly all clupeiform entries and were regarded as either "chum" or bait because they occurred only in the hook-and-line specimens. Perciform prey included a flatfish and a juvenile giant kelpfish, each several inches in length. Limbaugh (*l.c.*) found crustaceans and smaller fish in their diet, and Fitch (*l.c.*) noted squid.

Treefish, *Sebastodes serriceps* (Figure 45)

One-fourth were collected by hook-and-line, the remainder were speared. All were from rocky areas at depths of 40 to 75 feet, during all seasons. Habitat broadly overlapped that of *S. carnatus* in the San Diego region yet the diet appeared to be much more restricted. Principal foods were shrimp (*Alphaeus dentipes, A. bellimanus, Spirontocaris*), crabs (*Pleuroncodes planipes*, cancroid, and spider), and perciform fish (unidentified). As with *S. carnatus*, adults commonly leave their caves and crevices to investigate a diver.

Cabezon, *Scorpaenichthys marmoratus* (Figure 46)

Over one-half were collected by spear, the remainder by hook-and-line. All were from rocky areas at depths of 40 to 80 feet, and represent all seasons. Principal foods were cancroid and spider crabs, octopus, and squid. Also making important contributions were "shrimp" (including a juvenile spiny lobster), gastropods (spiral-shelled and nudibranchs), and fish (one eel-blenny, a juvenile giant kelpfish, and unidentified fish eggs). Algae, including fragments of reds and greens, were undoubtedly taken incidentally to the other items. These data agreed quite well with O'Connell's (1953) finding that crabs are the principal food. The indicated importance of abalone and limpets vs. cephalopods was reversed. Small perciform fishes and fish eggs were equally important in both studies. The general findings also agreed with those of Limbaugh (*l.c.*). No other investigators have recorded the occasional presence of rocks in cabezon stomachs, as noted by Limbaugh (personal communication).

Lingcod, *Ophiodon elongatus* (Figure 46)

Eleven were taken by hook-and-line and six by spear, during all seasons. Specimens came from rocky areas at depths of 25 to 125 feet. The diet was almost entirely fish and squid. Algal fragments occurred together with the remains of one large percoid fish and probably represent food from the prey (another lingcod taken at the same time contained a fresh halfmoon which typically contains large quantities of algae). Engraulids occurred only in the hook-and-line captures and some were well-digested. Perciform entries included one topsmelt. Fitch (*l.c.*) noted that the young feed on shrimp and other crustaceans. The lingcod is strictly demersal and lacks an air bladder. Adults commonly rest motionless on rocky ridges or rises. They swim with a sinuous motion.

Painted Greenling, *Oxylebius pictus* (Figure 46)

Nine specimens were poisoned, the remainder speared. All seasons are represented. Collections came from rocky areas at depths of 30 to 80 feet. Only one size-group was taken (the three bars figured represented collections from different seasons). The data represented by each lowermost bar-diagram should be interpreted with caution, because the fish were mainly from a collection in which the kelp canopy was inadvertently poisoned nearly a half-hour before effects reached the bottom, so that some canopy invertebrates, especially *Idothea resecata*, probably became unusually available. Principal foods were

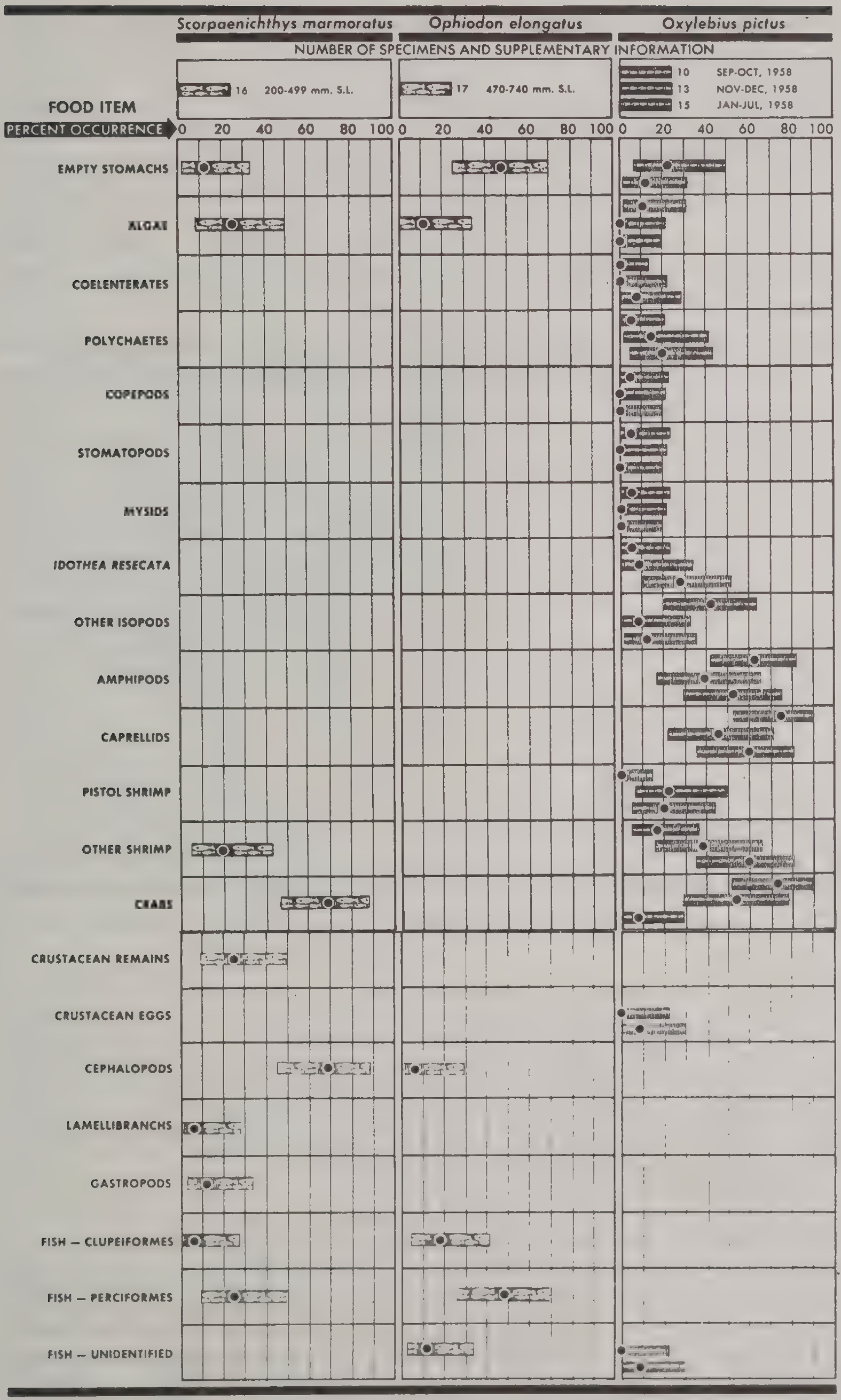

FIGURE 46. Food of the cabezon, lingcod, and painted greenling.

small demersal crustaceans and polychaetes. Cancroid and spider crabs were represented nearly equally. Shrimp included bent-back *Spirontocaris, Betaeus* spp., and pistol types (*Alphaeus dentipes* and *A. bellimanus*). A wide variety of other amphipods occurred, including *Caprella* sp. and many elongated forms with large chelae. Isopods were principally flabelliferan. The single fish entry was for eggs in the eyed stage. Similar to cottids, this species is strictly demersal and lacks an air bladder. Although sometimes common about rocky floors under kelp beds, they were never observed separated from rocky substrate. The males are pugnacious and have been observed to dart a foot off the bottom to nip a passing fish many times their size.

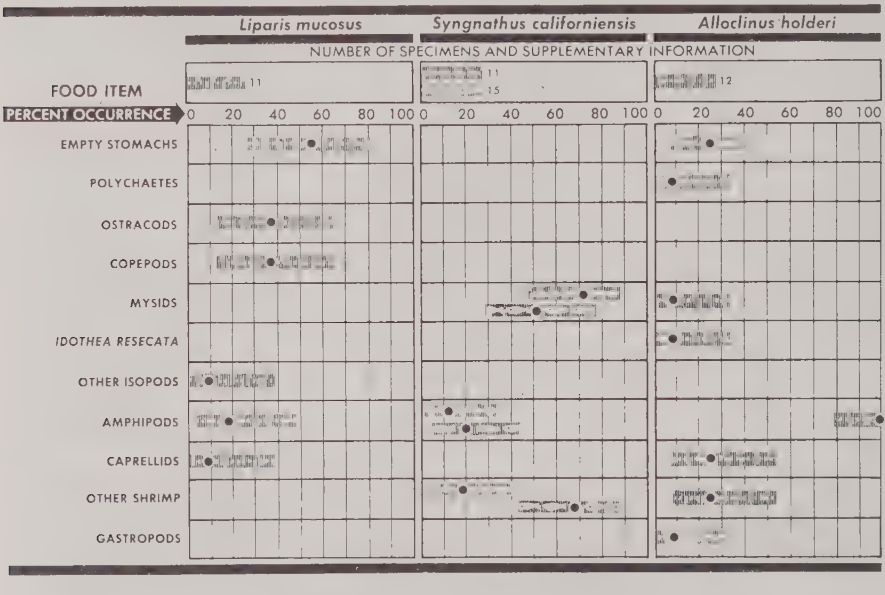

FIGURE 47. Food of the slimy snailfish, kelp pipefish, and island kelpfish.

Slimy Snailfish, *Liparis mucosus* (Figure 47)

All specimens used were collected by rotenone from the Papalote Bay kelp bed, 10 August 1959. Depth of capture was 32 feet. This species occupied kelp holdfasts, and the Papalote Bay specimens probably originated from this habitat. A microcarnivorous diet was indicated, with feeding mainly on small surface-associated crustaceans, probably made available by the poisoning.

Kelp Pipefish, *Syngnathus californiensis* (Figure 47)

All specimens used were picked from freshly cut kelp being taken aboard a kelp harvester near Gaviota on 26 May 1960. Stomach fullness was not assessed because a definite stomach is lacking. Principal foods were mysids and small shrimp, both of which abounded in the kelp canopy at the time of collection. Small amphipods were also frequent. Limbaugh (*l.c.*) noted chiefly mysids and small amphipods for this species.

Island Kelpfish, *Alloclinus holderi* (Figure 47)

Specimens used were taken by rotenone at 32 feet in the Papalote Bay kelp bed on 10 August 1959. The species is bottom-dwelling. Because the kelp-bed canopy was accidently poisoned first, the data may be seriously biased toward canopy-inhabiting crustaceans. All specimens had eaten small gammarid amphipods; small shrimp and caprellids were of secondary importance.

Spotted Kelpfish, *Gibbonsia elegans* (Figure 48)

Samples were obtained by rotenone from kelp beds, in July, August, and November 1959. Both *G. elegans* and *G. metzi* mimic habitat coloration and a color analysis of the Papalote Bay specimens suggested that the majority of the *G. elegans* specimens came from the kelp columns and coralline algae (82 of 106 specimens were mottled red-and-black or red-and-white, a pattern normal for the coralline-algae habitat; 14 had light-tan ''kelp'' coloration, and probably were residing in the kelp sporophylls or stipes, and 10 were dark-red and may have been residing in holdfasts or crevices). An aquarium-held specimen obtained from a holdfast (70-foot depth) was dark-red but changed to a mottled grey, similar to that of the aquarium substrate, within 2 or 3 days. In contrast, all specimens of *G. metzi* from the Papalote Bay collection were light-tan or mottled tan, suggesting that the entire sample was from the kelp columns.

Principal food was small flabelliferan isopods. Of secondary importance were polychaetes, small *Idothea resecata* (and *I.* spp.), gammarid amphipods, caprellids, shrimp (pistol and other types), crabs (megalops, hermit, spider), and small gastropods (dove shells). The data should be interpreted with caution, however, because all specimens were collected by rotenone methods. Limbaugh (*l.c.*) listed crustaceans and mollusks, and similar observations were made by Mitchell (1953) on 72 intertidally-collected specimens. Metz (1912) noted small mollusks (especially limpets), crustaceans (crabs, amphipods, etc.), minute worms, and foliose red algae in tidepool specimens.

Striped Kelpfish, *Gibbonsia metzi* (Figure 48)

The sample was obtained by rotenone at Papalote Bay, 10 August 1959. Specimens probably had resided off the bottom in the kelp, because they were uniformly kelp-colored, in contrast to the predominant coralline coloration of *G. elegans* (described above), and because only this species is taken by the kelp harvesters, and is consistently so taken (Carl L. Hubbs, personal communication). Principal foods were *Idothea* spp. (mainly *resecata*), and assorted small amphipods. Small isopods, shrimp, and copepods were secondary in importance. Unidentified fish eggs also were noted.

In comparison with *G. elegans*, the food composition for *G. metzi* appears richer in items known to be abundant about kelp fronds and stipes, particularly *Idothea resecata*. The absence of mysids from the diet of both *Gibbonsia* species is unexplained. Limbaugh (*l.c.*) stated only that *G. metzi* feeds on small crustacea in the canopy biotope. Mitchell (1953) identified *Idothea* (three spp.), assorted amphipods, shrimp (two spp.), and worms, in 17 tidepool specimens.

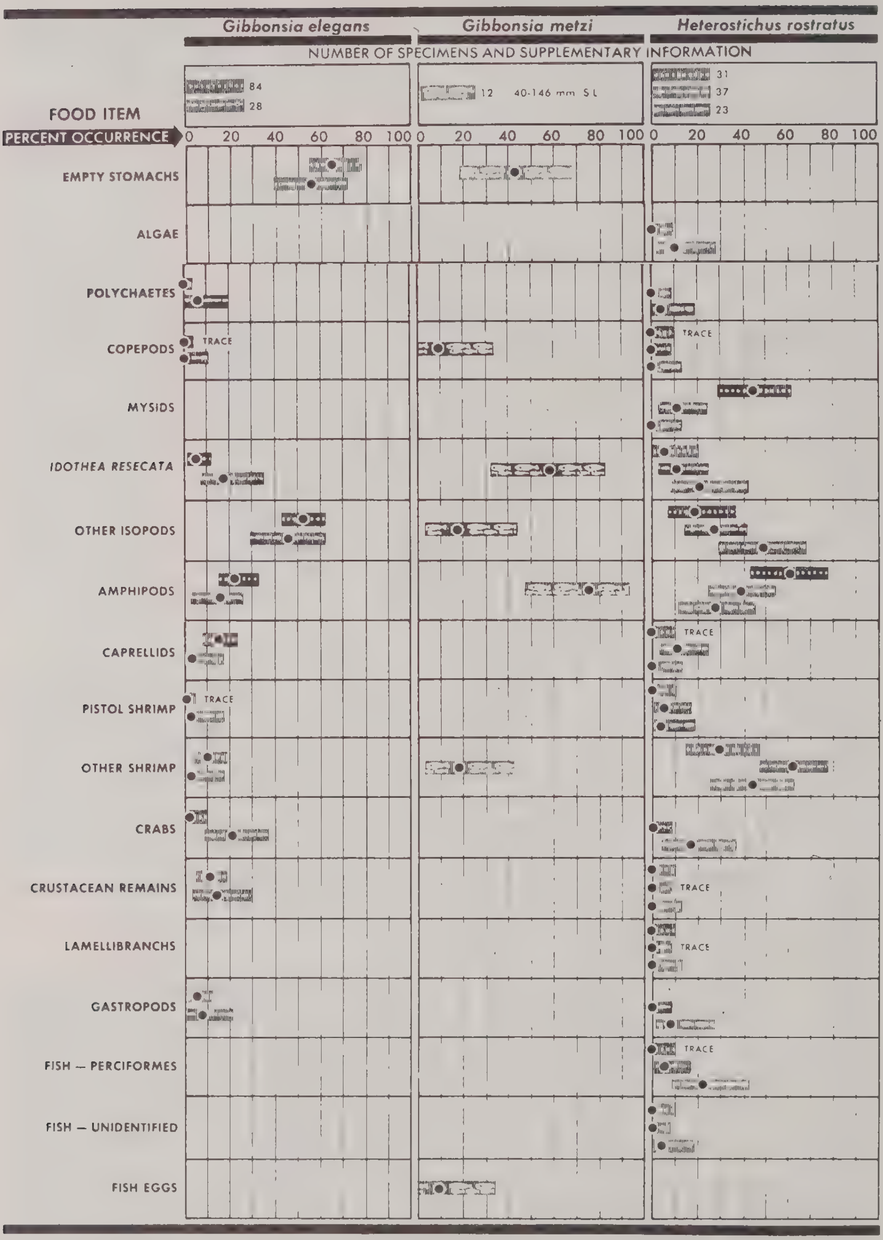

FIGURE 48. Food of the spotted kelpfish, striped kelpfish, and giant kelpfish.

Giant Kelpfish, *Heterostichus rostratus* (Figure 48)

Nearly all specimens used were from three kelp-bed rotenone collections in July, August, and November 1959. Depths ranged from 25 to 35 feet. Giant kelpfish attain high concentrations in kelp columns and canopies, but individuals are not readily seen, because they resemble kelp fronds in both shape and coloration. Individuals also are common about laminarian algae and eel grass on the bottom. They are expert mimics of their habitats, which they match in pattern, hue, and value, and often in attitude.

Principal foods were mysids, isopods (including *I. resecata*), amphipods, and shrimp (other than pistol shrimp), all of which abound about kelp. Pistol shrimp were secondary in importance but indicated that some individuals forage near the bottom. Mysids and small amphipods became less important with increase in fish size but consumption of isopods and fish increased. Fish items included *Rimicola eigenmanni,* señorita (small-sized), giant kelpfish (postlarval), kelp perch (juvenile), cottids, and slimy snailfish. Crab entries were principally spider forms. Limbaugh (*l.c.*) noted crustaceans as important in their diets, and small fish and mollusks also occurred. Metz (1912) found "soft crustacea (amphipods and isopods)" in a few intertidal specimens.

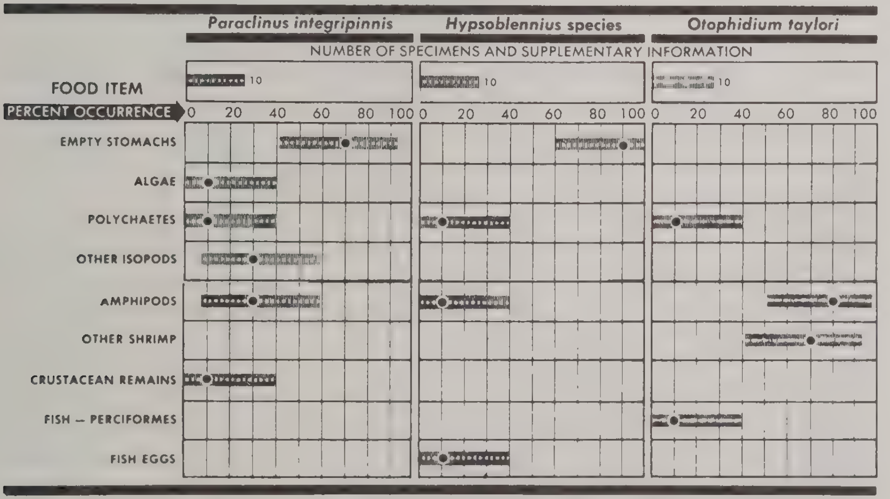

FIGURE 49. Food of the reef finspot, mussel blenny, and spotted cusk-eel.

Reef Finspot, *Paraclinus integripinnis* (Figure 49)

Specimens used were poisoned in a kelp bed 25 feet deep in July 1959. Little is known concerning the habits of this species, but the specimens probably inhabited short algae at the collection site. Small isopods and amphipods were principal foods.

Mussel Blenny, *Hypsoblennius* sp. (Figure 49)

Specimens used were poisoned in a kelp bed 25 feet deep in July 1959. Nearly all specimens had empty stomachs. One contained polychaetes, another amphipods, and a third unidentified eyed fish eggs.

Spotted Cusk-eel, *Otophidium taylori* (Figure 49)

All specimens used were from the Papalote Bay collection in August 1959. Specimens originated from a region of mixed sand and rock at 32 feet. Important food items were shrimp (other than pistol shrimp) and small amphipods. Other foods included the remains of a polychaete and a 16-mm (SL) cottid. Because sections of the kelp canopy were inadvertently poisoned first, normal forage items may have been contaminated with canopy organisms.

TABLE 29

Relative Utilization of the Food Categories by the Entire Fish Fauna

All species and their size-groups considered separately. All means for occurrence (Figures 35 to 49) classified and weighted as follows: 1 = 2 percent or less; 2 = 3–24 percent; 3 = 25–46 percent; 4 = 47–68 percent; 5 = 69 percent or over. Intensity represents the average for occurrence-classes in fishes showing the item, and gives a measure of average intensity of consumption. Dispersion represents the breadth by which the item is used by the fauna, where *f* represents the fish size-groups showing the item out of the maximum number, 92 (F), possible. The utilization index is a product of A and B. Items utilized both intensively and extensively within the fauna will give high values. Items appearing at low frequencies and only in a small portion of the fauna will give low index values. Items through cephalopods arranged in order of decreasing utilization index.

	Intensity	Dispersion	Utilization index
Item	(A = $\overline{X}$)	(B = f/F)	(A × B)
Gammarid amphipods	2.7	.61	1.65
Crabs*	2.7	.50	1.35
Algae*	2.8	.45	1.26
Other shrimp	2.1	.60	1.26
Polychaetes	2.2	.53	1.17
Fish—Perciformes	2.1	.42	.88
Other isopods	2.2	.38	.84
Caprellids	2.2	.37	.81
Idothea spp.	2.0	.40	.80
Gastropods	2.0	.37	.74
Lamellibranchs	2.5	.29	.72
Mysids	2.2	.32	.70
Fish—Clupeiformes	2.3	.29	.67
Bryozoans	2.2	.26	.57
Pistol shrimp	2.0	.28	.56
Copepods	2.2	.23	.51
Ophiuroids	1.8	.25	.45
Echinoids	2.5	.14	.35
Ostracods	2.0	.16	.32
Cephalopods	2.0	.15	.30
Coelenterates	1.6	.05	<.20
Platyhelminths	2.0	.01	"
Echiuroids	2.0	.01	"
Sipunculids	2.0	.01	"
Branchiopods	2.0	.02	"
Cirripeds	2.0	.04	"
Stomatopods	1.7	.07	"
Cumaceans	2.0	.01	"
Insect larvae	2.0	.02	<.20
Crustacean eggs	2.7	.04	"
Pycnogonids	2.0	.01	"
Gastropod eggs	2.0	.01	"
Asteroids	2.0	.03	"
Holothurioids	1.7	.03	"
Tunicates	1.7	.03	"
Branchiostoma	2.0	.01	"
Fish eggs	2.0	.03	"
Crab larvae	2.0	.01	+

* Bimodal distributions.

IMPORTANCE OF THE FOODS

If frequencies of the food items are considered, as well as the number of species and size categories utilizing them, a general hierarchy of utilization may be constructed (Table 29). Because the data are not weighted for relative nutritional value, volumes, and digestion rates, only general trends are indicated.

Gammarid amphipods had the highest index of utilization in the study. Representatives of this group were nearly ubiquitous in the inshore environment and were abundant in bottom algae, kelp holdfasts, and about kelp fronds and stipes. Sixty-one percent of the frequency diagrams recorded their presence. They were very heavily utilized by some or all samples of black perch, island kelpfish, striped kelpfish, and spotted cusk-eel. Also utilizing gammarid amphipods heavily, but to a lesser degree, were California sargo, kelp perch, rubberlip perch, painted greenling, and giant kelpfish.

Crabs had a utilization index nearly as high. They differed from gammarid amphipods in having a bimodal frequency distribution of intensity-of-usage values. Modes occurred at 2.5 and 4.5 which indicated that in addition to utilization at medium rates by many species, several fish concentrated heavily on this item. Interpretation of the values is complicated because the pelagic red crab was abundant both in the kelp beds and in the stomach samples during spring, 1959. Fish that contributed to the 4.5 mode for intensity were black croaker, rubberlip perch (one size-group), pile perch (two size-groups), California sheephead (100–199 mm size-groups), gopher rockfish (two size-groups), and painted greenling (two samples). As noted previously, crab entries for pile perch were principally hermit crabs.

Algae also gave a bimodal frequency distribution for intensity-of-usage classes. An upper mode (5.5) reflected high occurrence in topsmelt (specimens less than 99 mm, seined from tidepools), garibaldi (all size-groups), and the reputed herbivores, the opaleye, halfmoon, and zebraperch. Algae entries contributing to the lower frequency mode (2.5) seem accountable to accidental ingestion with animal prey items and fragments being mistaken for fish prey.

Shrimp other than pistol shrimp gave a high index of utilization. This was to be expected because, like gammarid amphipods, shrimp are widespread and abundant in the inshore environment. Shrimp were heavily utilized by kelp pipefish and kelpfish among the kelp-inhabiting fishes and by the spotted cusk-eel and painted greenling (one sample) among bottom-dwelling species.

Polychaetes showed high occurrence only once (black perch, 100 to 199 mm, June to October 1958). In general the polychaete data were not very conclusive because of the diverse forms and ecology of the group and the scant remains usually recovered (some identifications were based on setae only). Perciform fishes showed narrower utilization by the fauna, as would be expected; a considerable variety of prey species was represented. Isopods other than *Idothea* spp. were heavily utilized by the giant kelpfish, which abounds in the kelp columns and canopy, and the spotted kelpfish, a bottom dweller. Although caprellids were abundant in the kelp canopy during some seasons, they were heavily utilized only by the black perch (100 to 199 mm size-group, for June to October 1958) and the painted greenling, both bottom inhabitants. Moderate frequencies for *Idothea* spp. occurred in the striped kelpfish only, and gastropods were not heavily utilized by any fishes. Lamellibranch entries were frequent in the pile perch and California sheephead, both of which have crushing pharyngeal plates. Principal lamellibranch species were kelp scallops and the swimming clam, *Lima*. Mysids were heavily utilized by California salema, kelp pipefish, and one adult specimen of vermilion rockfish. Clupeiform entries were of high frequencies only in sand bass of the 300 to 399 mm size-group and barracuda, and the data may represent bait or ''chum.'' Bryozoans and pistol shrimp were not frequent in any fishes. Pistol shrimp, however, may be important to some such as the kelp bass, because of the relatively large size and continuous low-level utilization. Copepods were taken in abundance only by blacksmith and ophiuroids were not utilized intensively by any fish species. Echinoids were of high occurrences in California sheephead and of low frequencies in numerous species. As noted previously, the recorded frequencies are probably biased toward high values in both hook-and-line and spear-collected specimens. Ostracods were infrequent in all species, and cephalopods were relatively common only in the cabezon.

Erratum: Page 112, line 18 up, for "Runula sp." read "a small blenny."

References for this paper follow reprint no. 131 in this volume.

9. EFFECTS OF KELP HARVESTING ON THE FISHES OF THE KELP BEDS

JAY C. QUAST
U.S. Bureau of Commercial Fisheries
Auke Bay, Alaska

INTRODUCTION

The beds of giant kelp along the Pacific coast of southern California and of Baja California, Mexico, represent important recreational areas to residents and visitors, as well as an important source of industrial products. These beds are focal points for commercial and private sportfishing parties in search of kelp bass, white seabass, and other bottom fishes, as well as such pelagic fishes as the yellowtail and barracuda. At times, especially on week-ends and holidays, the sportfishing boats crowd the areas in and about the beds. In addition, increased numbers of skin divers and SCUBA divers are discovering the beautiful underwater vistas of the kelp beds and their abundant and varied fishes. Scenes comparable to those of the lush redwood forests of the Pacific Northwest are available a mere few hundred or thousand feet from the semi-desert shores of the Californias. Although the kelp beds are important recreational areas today, they will become vital in the future, when vastly greater numbers of people make southern California their home or recreation center.

With the development of SCUBA, the world of the kelp beds has been made available not only to the spearfisherman, artist, and photographer, but also the biologist. For well over a decade now, the kelp-bed environment has been studied by diving biologists at the Scripps Institution of Oceanography and other centers of marine research. Primary motivation has been the requests from two groups vitally concerned with the welfare of the kelp beds and their fauna; the companies harvesting kelp and the organizations of sportfishermen. A principal factor spurring research has been the necessity for information on any effects harvesting may have on kelp and on the rich fish fauna of the beds. The knowledge gained in answering this problem, however, has gone beyond merely outlining the interrelationships between kelp harvesting and the fishes. Basic knowledge has also been gained toward the intelligent management of a large segment of the fish resource of California, in anticipation of the much heavier usage the resource will surely receive in the future.

This report summarizes previous knowledge on this problem and findings of the 5-year IMR Kelp Program. In general, the studies continue those of Conrad Limbaugh, pioneer underwater naturalist at Scripps. Detailed reports of the scientific findings forming the basis for this summary are given in Chapters 5 through 8 of this bulletin.

The Limbaugh report, ''Fish life in the kelp beds and the effects of kelp harvesting'' (Limbaugh, 1955) summarized investigations conducted from 1948 to 1954, primarily by this single acute investigator.

Reprinted from California Department of Fish and Game, Fish Bulletin 139, 1968.

The kelp environment was surveyed, qualitative studies were made on the food and biology of the fishes, and kelp harvesting was analyzed for direct effects. In his summarizing report Limbaugh stated, ''As a result of these long and thorough studies, it is concluded that kelp harvesting, as currently practiced, has no seriously detrimental effects on fishing.'' Because Limbaugh's studies were of a survey nature many questions were not conclusively answered. ''Seriously detrimental effects'' were not defined. The food studies are of limited value because no indication was given concerning the number of specimens examined, and because the food data are not evaluated in regard to collection methods, seasons represented, or whether both the stomach and intestine were examined. However, the work was very important as a first step in the ecological studies of kelp beds and their fishes.

A succeeding study on the problem was conducted by David H. Davies, after a year with the kelp program and constitutes the following Chapter (10) of this bulletin. Comparisons were made between amounts of kelp harvested commercially and numbers of fish taken by fishermen aboard sportfishing boats. Statistics were compared within the boundaries of oceanic statistical squares used by the California Department of Fish and Game to delineate all fishing waters along the coast of southern California and include all of the kelp beds as well. Data for 1947 through 1956 were analyzed by means of graphical and correlation analysis. Davies concluded ''there is no apparent adverse relationship between the total sportfish catch per unit effort and the amount of kelp harvested'' and ''the frequency of harvesting operations in the kelp beds has no adverse effect on sportfishing.'' The findings of Davies did not eliminate the need for further research and in any case the fishery statistics are difficult to evaluate accurately. However, the general conclusions are justified and agree with those of Limbaugh.

Because many gaps of knowledge remained in regard to the central question, further studies were undertaken by the Kelp Program. Quantitative studies were made on the food of the kelp-bed fishes, with particular attention to the kelp bass, and on the size, composition, and habitats of the fish crop.

FINDINGS

In commercial kelp harvesting, the kelp in the surface 4 feet of water is cut from the plant below by a large set of mower-like blades, of special harvesting vessels, drained of excess water, and loaded by means of conveyer belts into a storage area for transportation elsewhere. The numerous ways in which such an operation may conceivably affect the kelp-bed fishes are discussed below, beneath the appropriate question headings. Effects on yellowtail, barracuda, and bonito, are not treated because these fishes are mainly pelagic and occur about kelp beds only incidentally.

1. *Does the harvesting of kelp destroy significant amounts of the eggs and larvae of fish species of actual or potential sport value?* This problem is discussed in detail in the Limbaugh report and my subsequent observations have substantiated his findings. No fishes of the sport cate-

gory attach their eggs to kelp. One forage species, the giant kelpfish, does attach its eggs to kelp, and also to seaweeds on the ocean bottom intertidally and subtidally. This species, though abundant in kelp beds, constitutes only a small fraction of the diet of sportfishes; removal of a small fraction of kelpfish progeny would presumably have little effect upon food chains leading to sportfishes. The giant kelpfish, while taken by the kelp bass in limited quantities, does not seem either to be as available or desirable as other similar-sized prey items such as squid, octopus, crabs, anchovy, and other fishes.

Although the larvae of fish may occasionally reach high concentrations in the kelp canopy, probably only a minimal fraction of their number is taken aboard a kelp cutter. The forward motion of the ship or barge creates strong currents and eddies about the kelp in the mowing blades, and these forces undoubtedly sweep a major portion of the swimming fishes and motile invertebrates from the blades and stipes. Also, the kelp is drained before it is stacked aboard the cutter, giving trapped organisms a second chance to return to the sea. Some of the kelp canopy is usually missed by the cutter, and some new canopy appears in the cutter's wake because the freshly cut plants are less bent by the pull of surface currents on their surface fronds. Both the kelp that remains or appears on the surface and the kelp remaining a few feet below are available as refuge to the displaced motile residents of the original canopy.

2. *Does the kelp cutting operation frighten sportfish from the area?* This question is also discussed by Limbaugh who states "Fishes are not driven away during harvesting operations. Diving has revealed them to be extremely plentiful just behind the kelp harvesters. Many species, including the kelp bass, are attracted by such disturbances in the kelp, and probably find extra food at that time." My observations verify those of Limbaugh. At normal kelp-bed depths fish show little concern when boats are operating overhead. Fish were observed to show no more fear of a kelp cutter than of a sportfishing boat, and the fish actually may be less disturbed by a kelp cutter because it operates at lower speeds. Even if fish were frightened unusually by the cutting operation and left the bed, they would undoubtedly return to their original surroundings when the disturbance ceased.

3. *Are significant amounts of fish food in the form of kelp, the organisms attached to the fronds and stipes of the plant, and trapped swimming invertebrates and fishes, removed by the harvesting operation?* This question was studied by Limbaugh and was also quantitatively investigated by Clendenning and Wing. Limbaugh concluded "The amount of invertebrate material brought on board attached to the kelp is so small in comparison with that left on the plants below the canopy that its absence can have little effect on the available food supply of the few fishes that feed on this material. Most of the free-swimming crustaceans and other fish-food organisms fall back through the screen." Studies by Clendenning and Wing showed that approximately one-third of the motile invertebrate animals that are associated with kelp fronds are taken aboard the kelp harvester. This value probably should be reduced to one-fourth or possibly less when

all forage animals are considered, because small fish are common in the canopy but were not included by the sampling procedure.

The relationship between kelp harvesting and the forage of the sportfishes may be roughly calculated, giving consideration to the probable effects of the most severe harvesting conditions. Both North and Clendenning (personal communication) agree that such circumstances are extreme and are probably rarely attained in actual practice; the calculations are presented merely to indicate maximal possible effects. In this calculation, it is assumed that 90 percent of the forage animals in a kelp bed are in the kelp canopy (Clendenning believed that 65 percent is a more reasonable upper limit), that the population of forage animals in the canopy is fully reconstituted in 3 months, and that the bed is cut three times a year. Under these conditions, for every 10 pounds of forage animals in the bed, 9 pounds are susceptible to removal. Of the 9 pounds of animals on the cut kelp, one-third or 3 pounds would be taken aboard the harvester and 6 pounds would return to the bed, leaving 7 pounds or 70 percent of the original animal material. On the basis of yearly loss, this 30 percent removal is roughly equivalent to a 15 percent loss when averaged over the 3-month period required for reconstitution of the canopy fauna (assuming that reconstitution is proportional to time). If three cuttings occur yearly, the maximum yearly loss would amount to:

$$\frac{\text{percent lost} \times \text{period of loss} \times \text{number of loss periods}}{\text{total time}}$$

or:

$$\frac{0.15 \times 3 \text{ (months)} \times 3 \text{ (harvests)}}{12 \text{ (months)}}$$

equals:

$$11 \text{ percent}$$

It must be emphasized that these figures represent maxima and include numerous assumptions too extreme for average conditions. Other assumptions that are included in the above calculations, but might be questioned, include the importance to sportfishes of the 3-month period allowed for full canopy recovery. It is possible that the canopy may be in its prime as a food source for fishes when it is quite open and long before it is fully recovered. A thin canopy may encourage the penetration of such forage fishes as topsmelt, anchovy, and sardine into the bed, and may render the inhabitants of the canopy more available to predaceous fishes.

Even the most severe conditions outlined above, in which the kelp bed is suddenly deprived of 30 percent of its forage animals, should not be seriously deterimental to the sportfishes, because they are surrounded by ample reserves in the form of motile animals that are either displaced from the canopy by the harvester or unaffected by the harvesting. For the kelp bass, these reserves in fishes alone, with examples of numbers found in underwater surveys, include kelp perch (up to 800 per acre), topsmelt (100-200 per acre), jack mackerel (100-500 per acre), giant and other species of kelpfish (150-550 per acre), pipefish, and numerous other species. Such reserves may be expected to buffer resident sportfishes adequately over the temporary periods of food shortage that are postulated.

Some kelp enters the diet of the fishes by way of intermediate animals, such as the kelp isopod (*Idothea resecata*), the kelp burrowing isopod (*Limnoria* sp.), and other invertebrate items such as gammarid amphipods and polychaete worms. The trophic relationships between these animals and kelp is described in California Water Quality Control Board, 1964. However, no fish is critically dependent on any of these invertebrates, and numerous alternative foods normally are available when any one item is absent. Among the kelp-eating forage items the kelp isopod is utilized most heavily by the kelp bass. Frequency-of-occurrence of this item ranges up to 20 percent (this food present in one out of five digestive tracts), but normally averages somewhere about 10 percent. Although large numbers of this isopod are frequent in the portion of a kelp bed that is harvested, the isopods are good swimmers and a large proportion of those that are in the canopy undoubtedly escape the kelp harvesters. Kelp isopods have been observed in good abundance in a kelp canopy approximately 1 week after the bed was harvested.

Kelp has been observed in quantity in the digestive tracts of only three species of fishes that are commonly associated with the kelp beds; opaleye, halfmoon, and señorita. Usually, adult opaleye are abundant about inshore rocky areas (from the surf zone to depths of 80 feet) and nearly every individual examined has its digestive tract packed with algae. Kinds of plants in the digestive tracts vary with the locality from which fish are taken. In shallow water, near the surf, adults usually contain moss-like reds and browns, while adults from kelp beds are usually stuffed with kelp. Similarly, kelp is frequently found in the digestive tracts of the halfmoon, but to a lesser degree than in the opaleye. Sometimes kelp may also occur in considerable quantities in señorita. However, the role of kelp in the diet of the three fishes is problematical, because examination of ingested kelp at the beginning and end of the digestive tract discloses that the kelp is altered remarkably little by the digestive process. Several attempts to demonstrate an enzyme capable of digesting kelp in the opaleye had negative results. A dozen half-grown fish confined in a tank and restricted to a diet of unencrusted kelp, gained no weight and died, apparently of starvation, within a month (see Chapter 8, this bulletin). Although these results are not conclusive, they offer some evidence that the kelp itself is not sought as food and that the three species may ingest algae primarily for the abundant animal materials present on its surface. Of the three fish species, the opaleye utilizes kelp most extensively and is of greatest importance to the sportfishery. It is taken primarily by surf fishermen in rocky areas. Population studies indicate that opaleye are usually most abundant from the shallower edge of the kelp beds to the surf, and it is unlikely that kelp harvesting would affect their populations adversely.

As a final note in regard to the relationship between kelp harvesting and the food of the kelp-bed fishes, it should be stated that thin specimens have not been encountered among the kelp bass, California sheephead, or opaleye that were sampled or observed. The observations include an intensive study made in an area that declined from a heavy bed of kelp to a barren region between the beginning of the study and 2 years later.

4. *Does harvesting of the kelp decrease the amount of fishes that can be carried by a kelp bed?* Studies by the Kelp Program disclose that kelp beds may carry over 300 pounds of fish per acre. However, nearly the same amounts of fish may be present in regions that are completely devoid of kelp but contain a rocky substrate of high relief, such as the underwater boulder slopes of Guadalupe Island. In contrast, the dense kelp bed at Gaviota, California, with an apparent abundance of animal foods in the canopy (mysids, kelp isopods) gave measurements of between 2 and 35 pounds of resident fish per acre, presumably because of the detrimental influences of a mud and sand substrate, or the bay-like environment. In regions with similar rocky substrates of low or moderate relief, the areas with kelp give estimates of the standing crop of fishes that is two to three times as great as that of similar habitats barren of kelp. These data indicate that kelp is not essential for the presence of large numbers of fishes in an area, but that it is conducive to a larger standing crop of fishes.

A favorable influence of kelp on the standing crop of fishes stems from the circumstance that the tall plants encourage bottom fishes to rise out of visual range of the ocean floor. The kelp columns serve as reference points away from the bottom in cloudy or murky water. Fish species that would be confined to the immediate vicinity of the bottom in a barren area are led, where kelp is present, to utilize the food resources present in the entire water column and at the surface. The removal of the canopy from a kelp bed is not regarded as detrimental because the bottom fishes still have the kelp columns available to facilitate their use of the entire water column.

Removal of the kelp canopy opens the bed, with the probable result that more forage fish of the upper water regions become visible and available to the predators below because they are silhouetted against the sky. It is also likely that an opening of the beds encourages their invasion by important baitfishes, such as the anchovy, sardine, and topsmelt.

For these reasons, it appears doubtful that the removal of the canopy of a kelp bed by harvesting decreases the desirability of the kelp bed to sportfishes. The loss of a fraction of the food is probably compensated for by other positive factors, and the fish undoubtedly are able to adjust to the change. Limbaugh tagged kelp bass in both the cut and uncut portions of a kelp bed near La Jolla and concluded "Obviously the tagged fish (in the harvested section) showed no significant tendency to seek refuge in the uncut area, despite the fact that the handled, marked, and often somewhat displaced fish would be expected to wander more than fish not so disturbed."

CONCLUSIONS

This report is the latest of three dealing with the relationship between kelp harvesting and the fishes of the kelp beds. Each study utilized different approaches to the problem: Limbaugh's, a qualitive survey; Davies', an examination of kelp-harvest and fishery statistics; and Quast's, quantitative studies on the food and populations of the fishes as well as further observations on their biology and ecology. All three investigators arrived at the same conclusion, namely that, within the limits of the methods used for study, no evidence has been obtained that kelp harvesting has a measurable effect on the fish populations. Although none of the three studies furnish complete proof that kelp harvesting is not detrimental to the fish populations, the agreement between the three investigations in regard to the relationships between the two factors bears considerable weight and must be considered seriously. It must be emphasized, however, that these conclusions apply only to what may be considered routine or normal harvesting practice, in which not over one-half of the kelp plant (linear dimensions) is taken by the harvester and no single bed is harvested more than three times a year. Because the weight of fishes in a specified inshore area is undoubtedly augmented by the presence of kelp, any process, natural or artificial, that reduces the areal extent of a kelp bed may be expected correspondingly to reduce the crop of fishes.

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Movements of Adult Lake Trout in Lake Superior[1]

INTRODUCTION

Returns from mature lake trout (*Salvelinus namaycush*) tagged in western Lake Superior in 1959 and 1962–65 described here suggest that trout disperse widely from the spawning grounds after spawning and return in subsequent years. Although the data were not extensive, returns from lake trout tagged near Keweenaw Point in 1950 and off Marquette, Michigan, in 1952 suggested similar movement (Eschmeyer, Daly, and Erkkila, 1952; Eschmeyer, 1955). Loftus (1957) stated that river-spawning lake trout of eastern Lake Superior returned annually to the same spawning streams. Movements of lake trout must be understood to manage and evaluate the rehabilitation of lake trout stocks in Lake Superior, especially when the trout move across interstate and international boundaries and are subject to different fishing regulations and fishing pressures.

MATERIALS AND METHODS

The 176 returns used in this study were from 1,221 lake trout tagged at Gull Island Shoal in western Lake Superior during the spawning runs of October 1959 and 1962–65. The fish were captured in gill nets of 4½, 5, and 6 inch mesh (stretched measure) set on the bottom in 6 to 8 fms. The total length of the fish ranged from 20 to 37 inches at tagging. Vinyl spaghetti tags with a numbered button were inserted through the epaxial muscle just posterior to the dorsal fin on 85 fish in 1959, 58, in 1962, 51 in 1963, and 62 in 1964. Plastic poultry leg bands of varying sizes were inserted around the lower jaw of 104 fish in 1963, 385 in 1964, and 476 in 1965. Because the percentage returns (1963 tagging) from the two types of tags were nearly identical, the data combines both tags. In computing percent returns, multiple recaptures were considered as a new recovery. Rewards were not offered for the return of tags. Recaptures were made by the Bureau of Commercial Fisheries, the Wisconsin Conservation Department, and by sport and commercial fishermen of Wisconsin and Michigan. Wisconsin and Michigan Conservation Department personnel assisted in returning the tags to the Bureau.

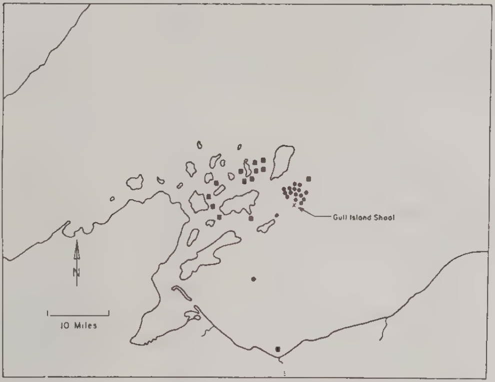

FIGURE 1.—Localities of recovery during November (dots), and December through March (squares) of fish tagged at Gull Island Shoal (X).

RETURNS

Of the 1,221 marked lake trout, 176 (14.4%) were recaptured. Most of the returns occurred during the first year at large; none were recaptured after 3 years. Of the total returns, 47% were recaptured in subsequent spawning runs at the tagging site and 53% were captured during the remainder of the year. The percentage returns given in Table 1 are not comparable among the various years of tagging because of differences in fishing effort during the spawning seasons and by the commercial fishery throughout the open season, and because of changes in abundance of the predatory sea lamprey (*Petromyzon marinus*) and its effect on the lake trout stocks during the years the fish were at large. The returns from the various sizes of tagged fish did not differ greatly (Table 2).

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[1] Contribution No. 373 of the Ann Arbor Biological Laboratory, U. S. Bureau of Commercial Fisheries.

TABLE 1.—*Percentage returns of lake trout tagged during the spawning run at Gull Island Shoal, in the Apostle Islands region of Lake Superior*

[Number of fish in parentheses]

Year tagged and locality of recovery	Number tagged	Percentage returns during years at large[1]			
		1	2	3	All years
1959	85				
Gull Island Shoal		1.2 (1)	0	0	1.2 (1)
Other areas		7.0 (6)	0	0	7.0 (6)
Total		8.2 (7)	0	0	8.2 (7)
1962	58				
Gull Island Shoal		5.2 (3)	0	1.7 (1)	6.9 (4)
Other areas		3.4 (2)	1.7 (1)	1.7 (1)	6.9 (4)
Total		8.6 (5)	1.7 (1)	3.4 (2)	13.8 (8)
1963	155				
Gull Island Shoal		8.4 (13)	2.6 (4)	0	11.0 (17)
Other areas		4.5 (7)	1.9 (3)	1.3 (2)	7.7 (12)
Total		12.9 (20)	4.5 (7)	1.3 (2)	18.7 (29)
1964	447				
Gull Island Shoal		4.9 (22)	3.1 (14)	–	8.0 (36)
Other areas		4.7 (21)	4.5 (20)	–	9.2 (41)
Total		9.6 (43)	7.6 (34)	–	17.2 (77)
1965	476				
Gull Island Shoal		5.0 (24)	–	–	5.0 (24)
Other areas		6.5 (31)	–	–	6.5 (31)
Total		11.5 (55)	–	–	11.5 (55)
All years	1,221				
Gull Island Shoal		5.1 (63)	1.5 (18)	0.1 (1)	6.7 (82)
Other areas		5.5 (67)	2.0 (24)	0.2 (3)	7.7 (94)
Total		10.6 (130)	3.5 (42)	0.3 (4)	14.4 (176)

[1] No fish were recaptured after 3 years at large.

MOVEMENTS

The distribution of the 176 recoveries from lake trout tagged at Gull Island Shoal show movements throughout the year. During the first month after spawning (November), most lake trout remained in the vicinity of the spawning area; from December through July they dispersed; and in August and September they moved back toward the spawning grounds. During the spawning period (October) nearly all returns were from the tagging site at Gull Island Shoal.

In November, the first month after spawning, 15 of 16 returns were within 5 miles of

TABLE 2.—*Length distribution of tagged and recaptured lake trout*

Total length (inches)	Year of tagging																	
	1959			1962			1963			1964			1965			All years		
	Number tagged	Returns		Number tagged	Returns		Number tagged	Returns		Number tagged	Returns		Number tagged	Returns		Number tagged	Returns	
		Number	Percent		Number	Percent		Number	Percent		Number	Percent		Number	Percent		Number	Percent
20.0–20.9	–	–	–	–	–	–	2	–	–	–	–	–	1	1	100.0	3	1	33.3
21.0–21.9	1	–	–	1	–	–	–	–	–	–	–	–	4	1	25.0	6	1	16.7
22.0–22.9	2	–	–	1	–	–	2	1	50.0	12	1	8.3	9	2	22.2	26	4	15.4
23.0–23.9	4	–	–	2	–	–	5	1	20.1	33	4	12.1	33	1	3.0	77	6	7.8
24.0–24.9	8	2	25.0	14	2	14.3	15	2	13.3	63	6	9.5	47	4	8.5	147	16	10.9
25.0–25.9	16	1	6.3	11	1	9.1	21	3	14.3	77	18	23.4	68	7	10.3	193	30	15.5
26.0–26.9	17	2	11.8	15	5	33.0	33	7	21.2	74	16	21.6	90	10	11.1	229	40	17.5
27.0–27.9	14	2	14.3	8	–	–	36	11	30.6	57	13	22.8	82	11	13.4	197	37	18.8
28.0–28.9	5	–	–	3	–	–	24	4	16.7	69	10	14.5	59	8	13.6	160	22	13.8
29.0–29.9	7	–	–	2	–	–	11	–	–	33	5	12.1	40	6	15.0	93	11	11.8
30.0–30.9	5	–	–	1	–	–	6	–	–	21	4	19.0	19	3	15.8	52	7	13.5
31.0–31.9	1	–	–	–	–	–	–	–	–	6	–	–	17	1	5.9	24	1	4.2
32.0–32.9	3	–	–	–	–	–	–	–	–	1	–	–	5	–	–	9	–	–
33.0–33.9	–	–	–	–	–	–	–	–	–	1	–	–	2	–	–	3	–	–
34.0–34.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
35.0–35.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
36.0–36.9	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
Totals	85	7	8.2	58	8	13.8	155	29	18.7	447	77	17.2	476	55	11.6	1,221	176	14.4

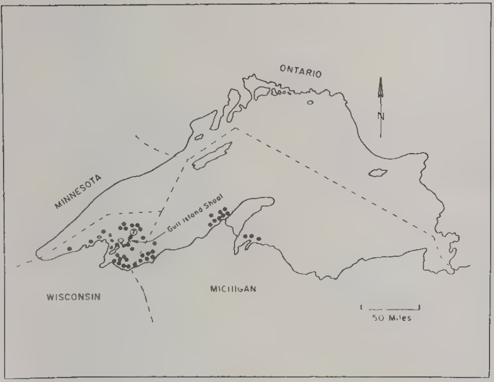

FIGURE 2.—Localities of recovery during April through July (dots) of fish tagged at Gull Island Shoal (X). The circled 7 indicates 7 recaptures.

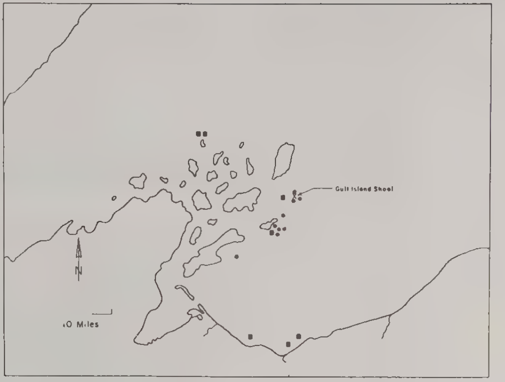

FIGURE 3.—Localities of recovery during August (squares) and September (dots) of fish tagged at Gull Island Shoal (X).

Gull Island Shoal (Figure 1, Table 3). The returns were concentrated there despite a commercial fishery operating in the Apostle Islands and along the south shore of Lake Superior.

Lake trout moved away from the shoal after November. The mean distance to point of recapture in December-March was 9.6 miles. Recoveries were made 5 to 25 miles from the tagging site but most returns were from the Apostle Islands region west of Gull Island Shoal. Lake trout may have moved in other directions from the shoal but nearly all commercial fishing, at this time of year, was west of the shoal. Lake trout continued to move away from the tagging site during April-July, when the mean distance to point of recapture increased to 33 miles (Figure 2). Most of the recoveries (73%) were within 25 miles of the shoal but eight were 70–90 miles and three were 100–120 miles from the shoal. During April-July, 19 fish were recaptured in Michigan waters of Lake Superior.

Recoveries in August-September indicated that lake trout were moving back toward Gull Island Shoal (Figure 3). The mean distance to point of recapture was 16.1 miles (range 5–25 miles) in August and 5.8 miles (range 5–15 miles) in September (Table 3). Although commercial gill nets were fished along the entire south shore of Lake Superior in August-September, no returns came from distances greater than 25 miles. With only one exception, all returns during the October spawning period were from Gull Island Shoal. The one fish captured on another spawning reef was originally tagged at Gull Island Shoal on 12 October 1965, recaptured and released at Gull Island Shoal on 13 October 1966, and was caught last on 27 October 1966 at another spawning shoal 12 miles

TABLE 3.—*Number of lake trout recaptured at different distances from the tagging locality in different months, 1959 and 1962–1965*

Month of recapture	Total returns	Miles to site of recapture[1] <5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120	Mean distance
November	16	15	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.1
December–March	14	1	8	4	–	1	–	–	–	–	–	–	–	–	–	–	–	–	9.6
April–July	48	2	8	8	5	12	–	1	–	–	–	1	–	3	5	–	2	1	33.0
August	7	1	1	–	2	3	–	–	–	–	–	–	–	–	–	–	–	–	16.1
September	9	4	4	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.8
October	82	81	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2
Total	176	104	21	15	7	16	–	1	–	–	–	1	–	3	5	–	2	1	–

[1] All distances are straight-line measurements from Gull Island Shoal.

away. Although the commercial fishing season for lake trout is closed during October, other spawning areas near Gull Island Shoal (within 7 to 20 miles) were fished by the Bureau of Commercial Fisheries and the Wisconsin Conservation Department but no other lake trout tagged at Gull Island Shoal were taken.

Only one of nearly 350 lake trout tagged by the Bureau and the Wisconsin Conservation Department at other spawning areas has been recaptured at Gull Island Shoal (unpublished data). The fish was tagged in October 1965 on a spawning reef near Basswood Island, 20 miles west of Gull Island Shoal, and was recaptured at Gull Island Shoal in October 1966.

Four lake trout tagged at Gull Island Shoal were recaptured there twice in subsequent spawning runs: Three tagged in 1963 were recaptured and released during the spawning runs of 1964 and 1965 and one tagged in 1962 was recaptured in 1965 and 1966.

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Jerold F. Rahrer

U. S. Bureau of Commercial Fisheries
Biological Station
Ashland, Wisconsin

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EFFECT OF BROWNLEE RESERVOIR ON MIGRATIONS OF ANADROMOUS SALMONIDS

Robert F. Raleigh and Wesley J. Ebel
Bureau of Commercial Fisheries
Fish-Passage Research Program
Seattle, Washington

Abstract

Spawning migrations of adult chinook salmon (*Oncorhynchus tsyawytscha*) were followed as they passed through the impoundments; their success in reaching the spawning grounds was compared with that of fish transported around the reservoir and released in the river above. Spawning success, as evaluated by data on egg retention, was also compared between groups of salmon that used the spawning grounds before and after construction of Brownlee Dam in 1958. On this basis Brownlee Reservoir evidently has little influence on spawning migrations of chinook salmon.

Seaward migrations of juvenile native chinook salmon and of hatchery-reared chinook salmon, coho salmon (*Oncorhynchus kisutch*), and sockeye salmon, were also studied as the fish passed through the impoundment area. Concurrent limnological studies revealed that physical and chemical factors restrict vertical distribution of migrants in the reservoir from early July through September. Surface temperatures increase and low values of dissolved oxygen move slowly upward from the bottom throughout the summer; these conditions limit the migrants to a narrow band of habitable water. Juvenile salmonids are almost absent from reservoir areas where zones of high temperature and low oxygen overlap. Except for a short period in late summer when a growth check was formed on the scales, growth rate of juveniles in the reservoir was good. Survival was extremely poor, however, for those smolts that did not complete their migration the first year. Reservoir and river conditions were separated in 1963 by a sharp line at the upper end of the reservoir. Most of the juvenile migrants accumulated above the line in the river water for 6 weeks, until conditions changed and the separation line disappeared.

Success of smolt migration was generally correlated with conditions of water flow through the reservoir. Well-oriented downstream currents depend not only upon water flows into and out of the reservoir, but also upon drawdown and pool length.

Introduction

BEFORE dams were built along the Snake River and its tributaries, the area above Brownlee Dam supported substantial populations of chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*), and steelhead trout (*salmo gairdneri*). Only remnants of the sockeye salmon populations now remain in the form of kokanee; those of chinook salmon and steelhead trout are greatly reduced. Fishery agencies saw construction of a proposed series of high-head dams on the Snake River as a possible serious threat to the remaining salmonid stocks in the system. Research was accordingly proposed to study the effect of the impoundments on the migrations of anadromous fish after completion of Brownlee Dam (the first in the planned series)in 1958.

Brownlee Dam was built to produce hydro-electric power and control floods. The level is therefore subject to large fluctuations that cause corresponding changes in reservoir length, depth, and current flow. The dam created a narrow, sinuous reservoir 56.5 miles long, less than 0.5 mile wide, and nearly 300 feet deep at maximum pool level (Figure 1). The Snake River above the reservoir drains a vast area of semi-arid irrigated farmland with moderate industrial development; water entering the reservoir thus contains a sizable load of organic and inorganic material.

Chinook salmon and steelhead trout returning to spawn above Brownlee Dam in the spring and fall were captured in a Buckley type fish trap at Oxbow Dam, a small regulating dam 12 miles immediately downstream from Brownlee. Some of the trapped fish were placed in a hatchery at Oxbow Dam; the rest were carried upstream around both dams by truck and released in Brownlee Reservoir to continue their migration to the spawning areas. Spring chinook salmon and spring and fall steelhead trout spawn in Weiser River and in Eagle Creek, a tributary to the Powder River. Fall chinook salmon spawn in the main Snake River, some 160 miles above the impoundment. The resulting young must pass through the reservoir on their seaward migrations. The juvenile fish migrate downstream as young of the year (age-group 0) from the Snake River population, and primarily as yearlings (age-group I) from the Weiser River and Eagle Creek populations.

The purpose of the study was to assess the effects of a large impoundment on the migrations of anadromous fish. Five related studies were of major interest: (1) physical limnology of the reservoir; (2) survival of adults migrating through the impoundment; (3) annual recruitment of juveniles to the reservoir; (4) behavior of the juveniles passing through the reservoir; and (5) annual escapement of juveniles from the reservoir. The study began in 1961 and was completed in the fall of 1965.

PHYSICAL FEATURES OF THE ENVIRONMENT

At full capacity, Brownlee Reservoir has a surface area of 15,000 acres and contains 1,470,000 acre-feet of water. Three main tributaries—the Snake, Powder, and Burnt rivers—and many small, intermittent streams enter the reservoir (Figure 1). The 14-mile stretch above the mouth of Burnt River is relatively shallow and much like a river. Depth increases below Burnt River; currents in the remaining 43 miles of the impoundment are very slow when the reservoir is at full pool.

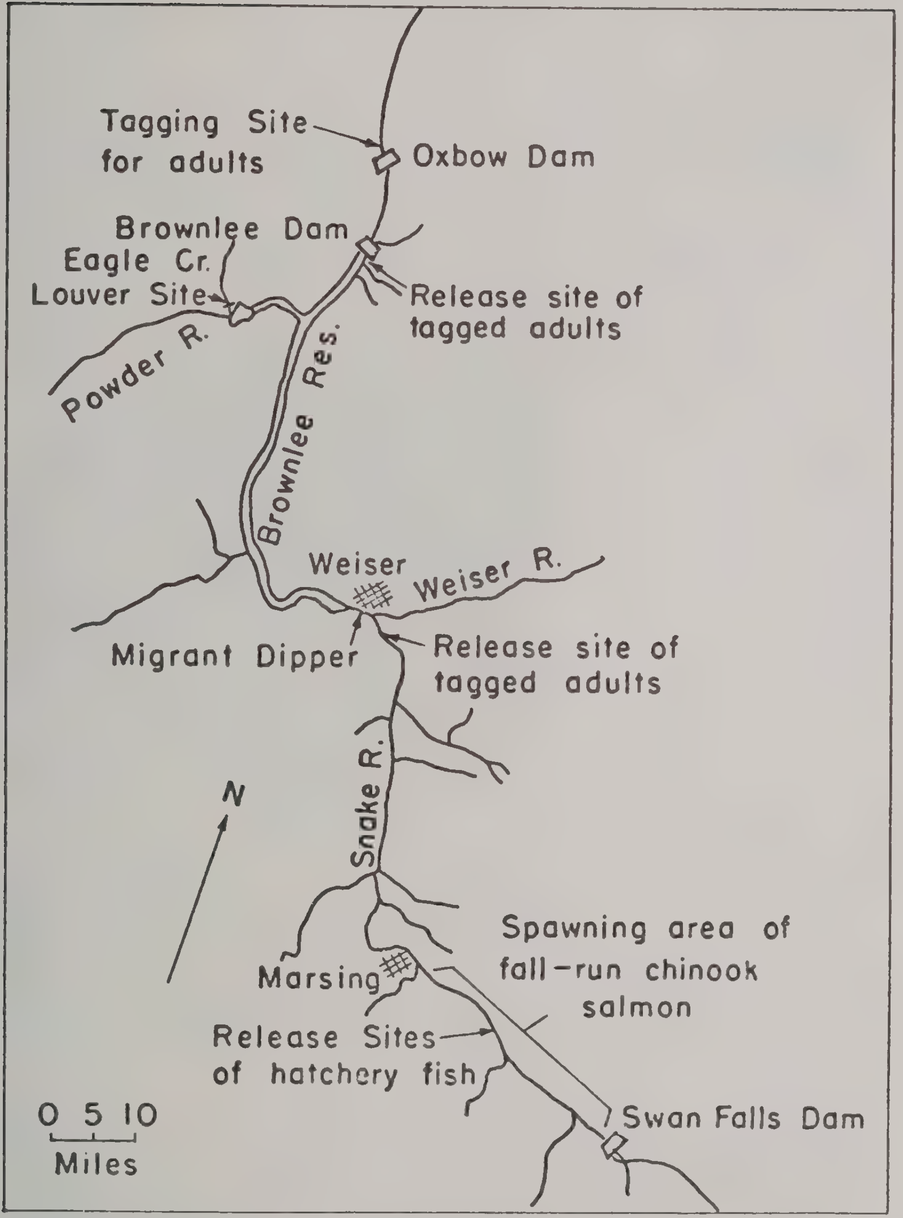

Tagging Site for adults
Oxbow Dam
Brownlee Dam
Eagle Cr. Louver Site
Release site of tagged adults
Powder R.
Brownlee Res.
Weiser
Weiser R.
Migrant Dipper
Release site of tagged adults
Snake R.
N
Spawning area of fall-run chinook salmon
Marsing
Release Sites of hatchery fish
Swan Falls Dam
0 5 10
Miles

FIGURE 1. Brownlee Reservoir with principal study areas.

Fluctuation in water level is considerable at Brownlee during late fall and winter. The reservoir is lowered as much as 100 feet depending on forecasts of spring runoff. Average volumes of water entering the reservoir from the Snake River range from about 9,000 cubic feet per second (cfs) in late summer to 40,000 cfs in the spring. Maximum flow during the study period was about 78,000 cfs. An important feature of a reservoir such as Brownlee is the depth at which the water is discharged. At Brownlee Dam, the turbine intake is 120 feet below normal pool level. The spillway discharges from 50 feet to the surface and also at a depth of 116 feet.

Water quality and currents, the primary environmental factors considered, were determined throughout the reservoir and at certain locations above and below it. All stations typically were visited at least once a month, but visits were weekly during critical periods.

Temperatures, conductivities, Secchi disc readings, and meteorological conditions were recorded at all stations. Water samples collected from the surface to the bottom were analyzed for oxygen, carbon dioxide, sulfate, turbidity, methyl-orange and phenolphthalein alkalinity, and pH. During the last year of study, nitrates and phosphates were also determined. Data on volume flow into and out of Brownlee Reservoir were recorded during each sampling period. Laboratory determinations were by standard methods (American Public Health Association, 1960).

Measurement of current velocity and direction started in the fall of 1963; three Sovonius-type current meters provided continuous monitoring and instantaneous readings. Although data are available on characteristics mentioned above, only the highlights of the temperature, oxygen, and current data are discussed here.

Temperatures and oxygen concentrations

Brownlee Reservoir differs somewhat from large, deep lakes, but nevertheless undergoes the seasonal changes typical of such lakes in the temperate zone: spring turnover, thermocline formation, fall turnover. Actual values of temperature, dissolved oxygen, and other factors vary considerably from year to year depending on (1) volumes of inflow and outflow, (2) reservoir drawdown, (3) length of filling period, and (4) weather.

The reservoir drawdown was minor (21 feet) in 1963, when filling was completed by early May. Changes from January to mid-March (Figure 2) were analogous to the "spring turnover," and isotherms were aligned vertically at temperatures from 33 to 42 F. Horizontal stratification began after mid-March and by early June a thermocline began to develop in the upper layers. A convergence line (Frey, 1963) also appeared in the upper reservoir at this time. Temperature and Secchi disc readings taken within a few feet of each other across the line were 61 and 65 F, and 1.8 and 4.0 feet, respectively. This line disappeared by late June. Summer stratification was complete by July 8, when the epilimnion, thermocline, and hypolimnion were

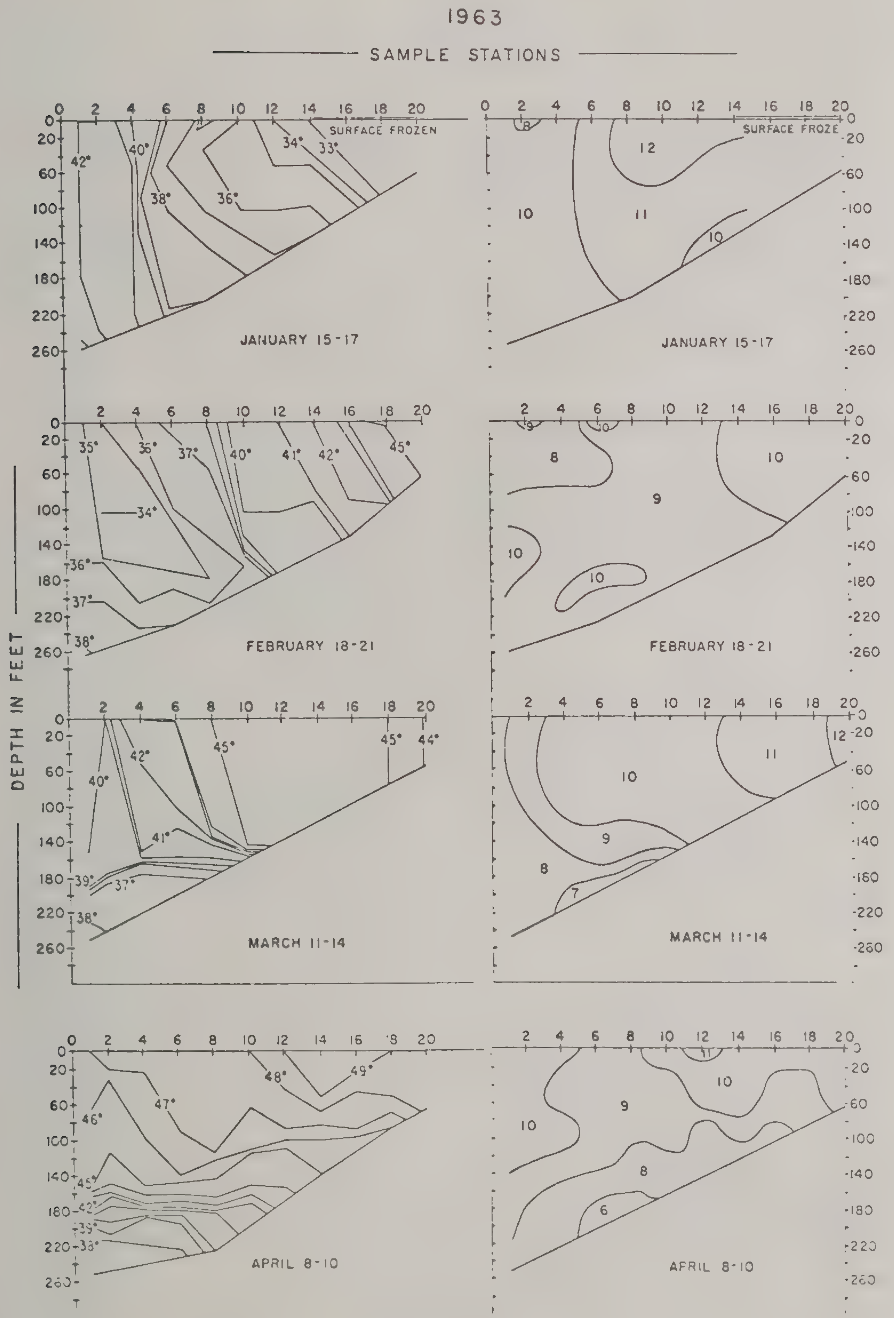


FIGURE 2. Isotherms (°F.) and dissolved oxygen levels in Brownlee Reservoir, January-December 1963.

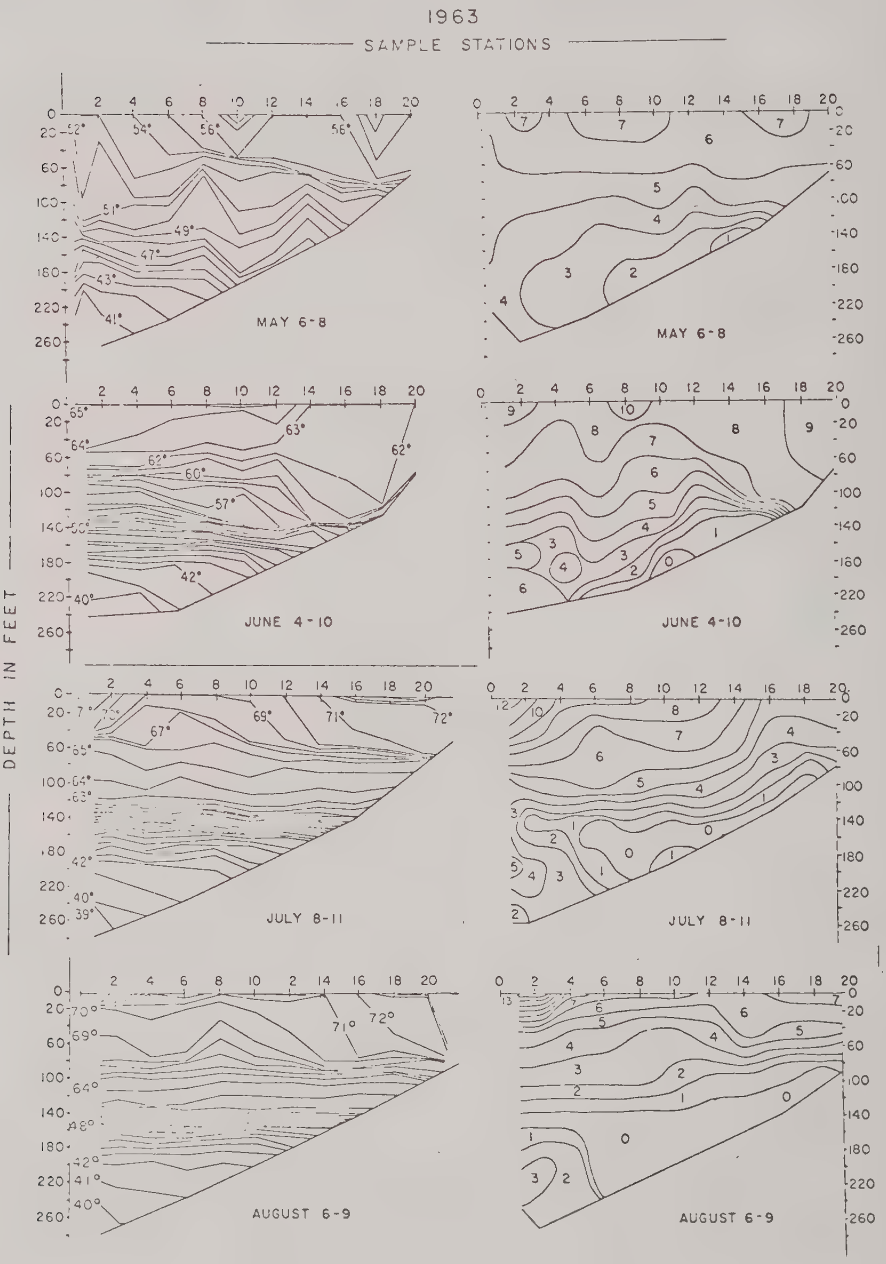
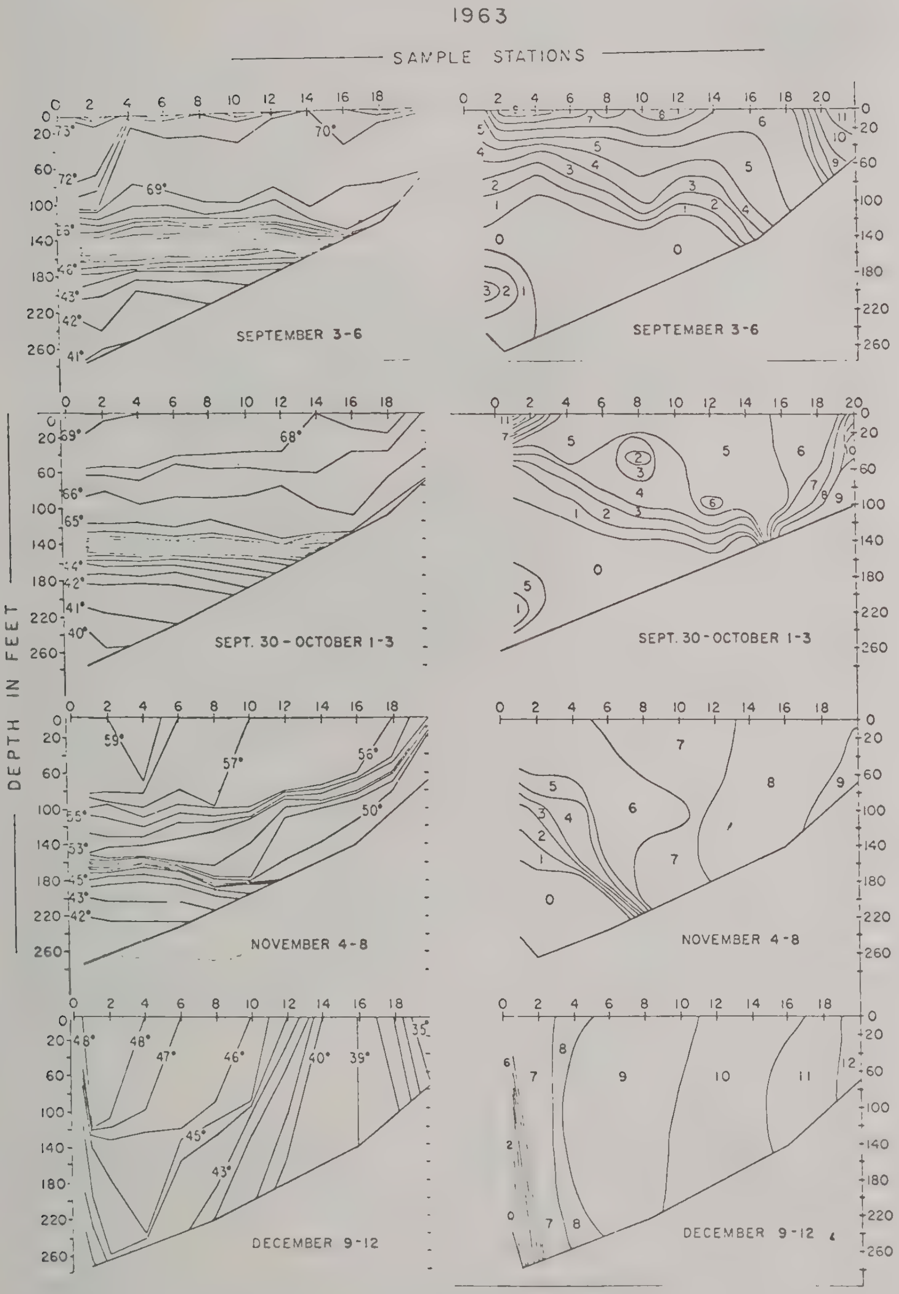


FIGURE 2a. Isotherms (°F.) and dissolved oxygen levels in Brownlee Reservoir, January-December 1963.


1963

SEPTEMBER 3-6

SEPTEMBER 3-6

SEPT. 30 - OCTOBER 1-3

SEPT. 30 - OCTOBER 1-3

NOVEMBER 4-8

NOVEMBER 4-8

DECEMBER 9-12

DECEMBER 9-12

FIGURE 2b. Isotherms (°F.) and dissolved oxygen levels in Brownlee Reservoir, January-December 1963.

well defined. Temperatures ranged from 39 F in the hypolimnion to 78 F in the epilimnion. In mid-October a convergence line was again formed. Dense, cool river water flowed under the warm epilimnion and evidently eroded the thermocline; only its remnants remained in November. By December 9, the reservoir was again turning over and isotherms were aligned vertically.

Dissolved oxygen approached saturation and was relatively stable from January to mid-March at all depths throughout the reservoir. Oxygen depletion started below the 160-foot level by March. This depletion continued until values were 3 ppm or less by August in all water below 80 feet, and 4 ppm or less in most of the water below 50 feet. Oxygen concentrations remained low through September but increased somewhat in the upper reservoir by October as a result of cooler inflow from the Snake and Burnt rivers. By November nearly two-thirds of the reservoir water had been replaced by water containing 7-9 ppm oxygen.

The seasonal changes in temperatures and oxygen concentrations occurred every year, but certain differences should be described. In 1965, a major drawdown (101 feet) and a prolonged filling period (not complete until mid-June) caused: (1) late formation of a thermocline, (2) warmer temperatures, 50 to 80 F, (3) lower oxygen concentrations during August and September, and (4) no sharply defined convergence line in spring due to increased currents. Drawdown was significant (89 feet) in 1964, but the filling period was somewhat shorter; temperatures and oxygen concentrations were more favorable than in 1965 but less favorable than in 1963.

Minor changes in oxygen concentrations and temperatures were also caused by differences in inflow-outflow volumes and weather. The amount of drawdown and the subsequent filling period, however, seemed to be the most significant factors in creating large differences from year to year in temperatures and oxygen concentrations. In all years, the most critical months for any salmonids that remained in the reservoir were August and September (Figure 2), when high (epilimnion) temperatures and low oxygen concentrations forced the fish into restricted and marginal habitats (Figure 3).

Downstream effect of Brownlee Reservoir

Brownlee Reservoir has a significant effect on temperatures and oxygen concentrations of the Snake River below Brownlee and Oxbow reservoirs. River temperatures below Brownlee Dam averaged 62 F during October or about 9 F higher than those in the river above the reservoir. Dissolved oxygen concentrations, however, averaged 3.6 ppm below the dam or about 5 ppm less than in the river above the reservoir (Figure 4). These changes in water quality are particularly important to fall-run salmon migrants because the reservoir delays the cooling cycle of the river and also reduces dissolved oxygen to near-critical levels for salmonids.

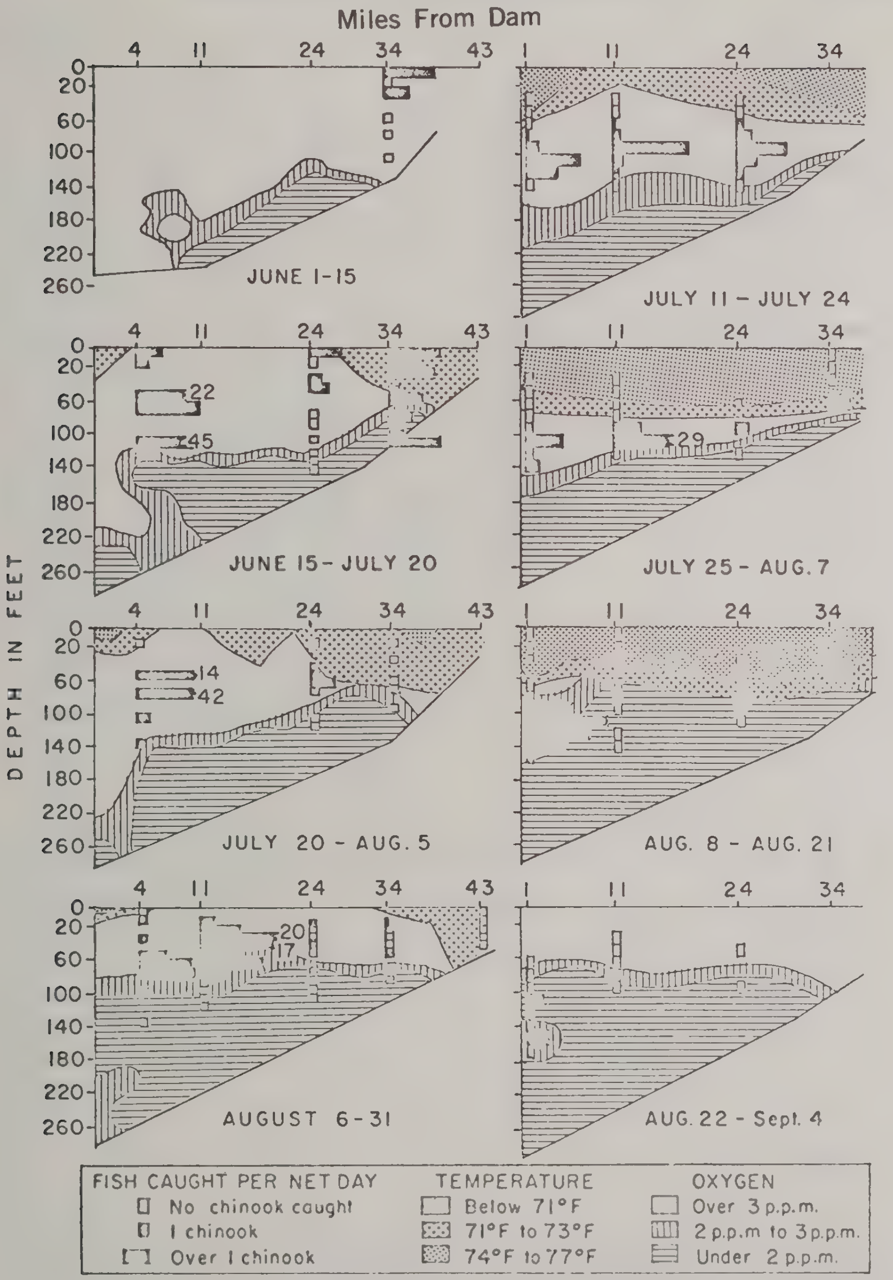


FIGURE 3. The vertical and longitudinal distribution of chinook stocks in Brownlee Reservoir in the summer of 1963 and 1965. Critical temperatures and oxygen levels are shown in relation to the catch per unit of effort. (Figures assembled from Durkin, Joseph T., 1966, unpublished manuscript.)

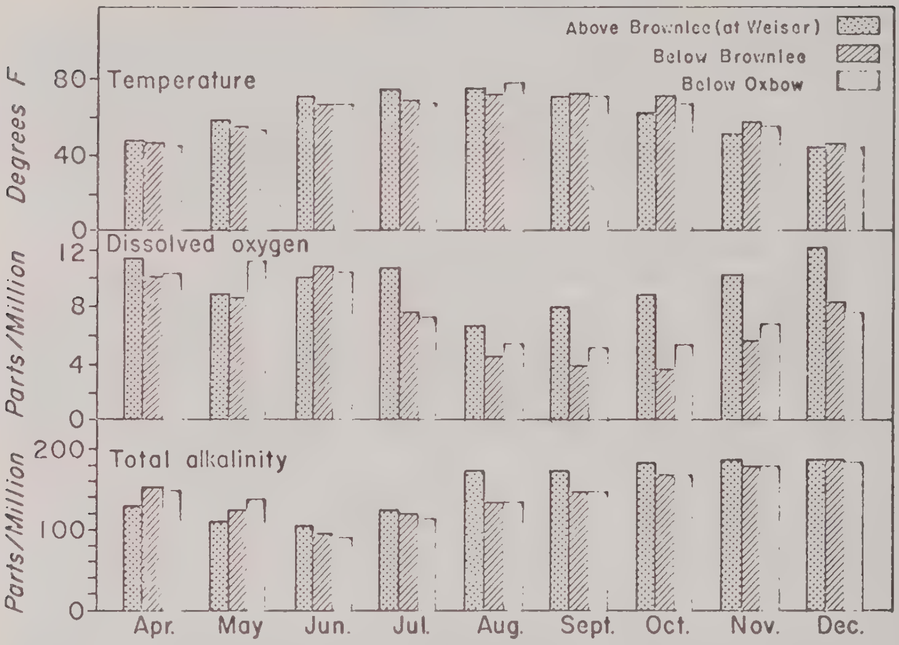


FIGURE 4. Comparison of temperature, dissolved oxygen, and alkalinity in the Snake River above Brownlee Reservoir, below Brownlee, and below Oxbow, 1963.

Current measurements

Continuous monitoring of surface currents in 1964 indicated significant changes in their downstream orientation and velocity during five reservoir stages: (1) maximum drawdown, (2) minus 44-foot level with high inflow and outflow, (3) fillup without spill, (4) full pool with heavy spill, and (5) full pool without spill (Figures 5, 6, 7, 8, and 9). Current conditions for downstream movement of salmonids were best during maximum drawdown and during the minus 44-foot level at high inflow and outflow. Although current measurements are available only from the fall of 1963 through 1965, they can be applied to the reservoir conditions in all years during times of fish passage. This use allows generalizations about the degree to which currents were favorable for salmonid migrations during different years.

Comparison of the years indicates that 1963 was much less favorable than 1964 and 1965 for passage of salmonid fingerlings during spring. Minimal drawdown and early filling created currents in the spring of 1963 that would have been similar to those recorded during periods of full pool, with or without spill (Figures 8 and 9). Downstream orientation of currents was weak and velocities were low during these periods. In 1964 and 1965, current velocities were relatively high and downstream orientation was good during most of the migration period because conditions similar to those shown in Figures 5 and 6 prevailed.

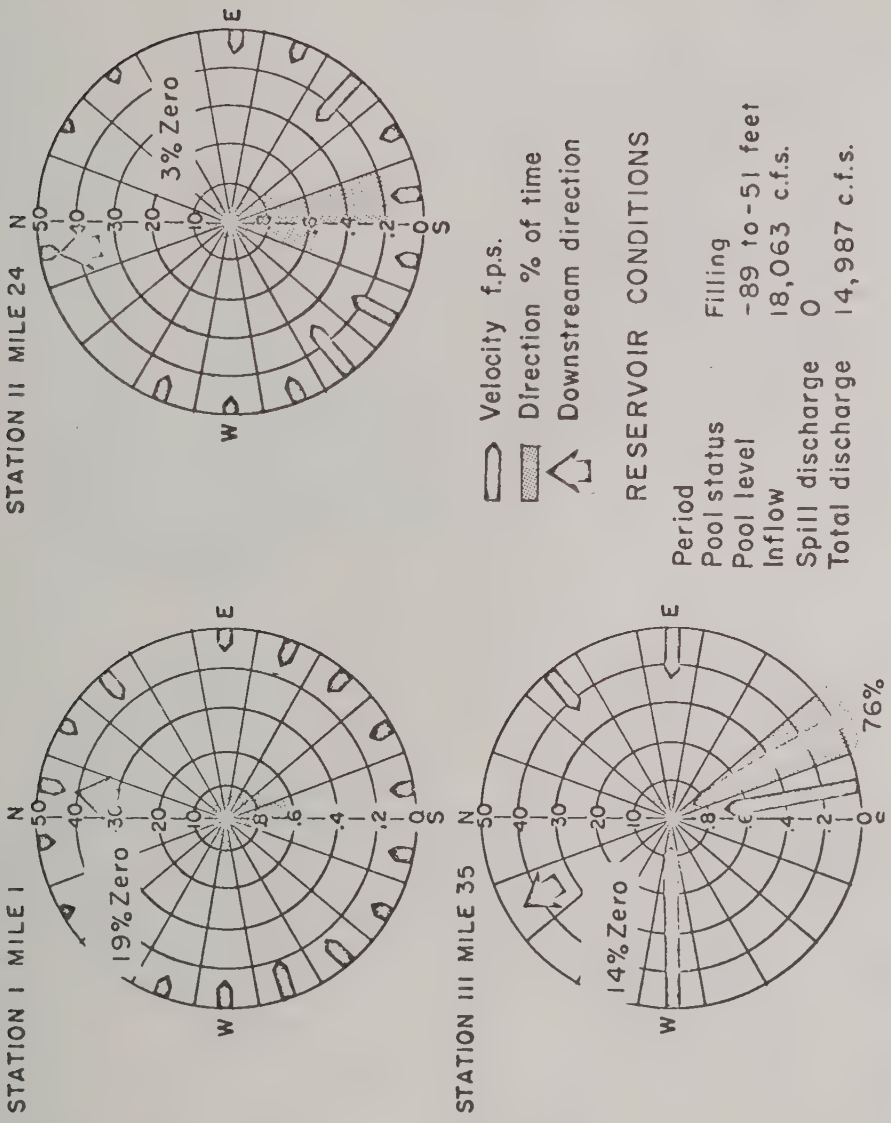
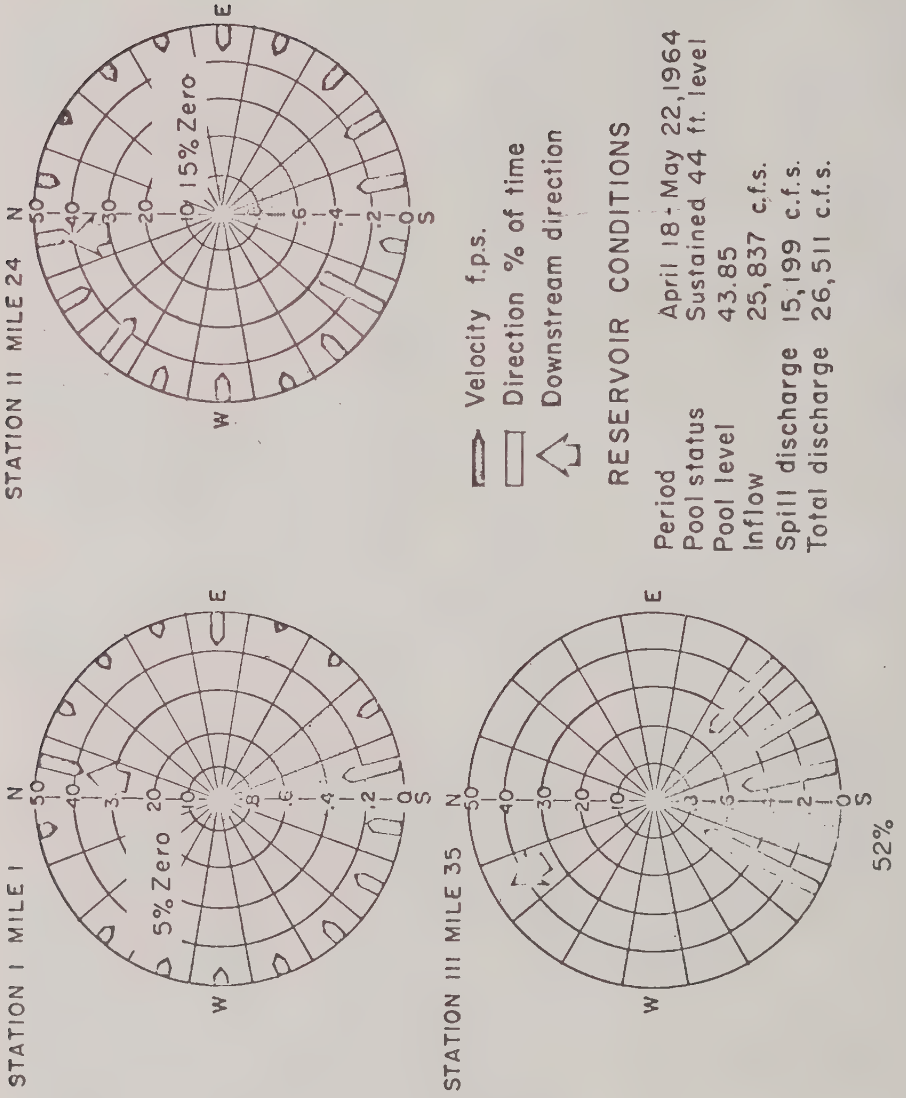


FIGURE 5. Direction (per cent of time) and average velocity (f.p.s.) of currents recorded at 10-foot depth in Brownlee Reservoir during period of maximum drawdown; March 6 to April 17, 1964. Direction of current reads toward point of wedge.

In summary, 1963 was a year of unfavorable currents, but 1964 and 1965 were favorable years for passage of migrants during spring. Environmental conditions for salmonids that did not leave the reservoir were more critical in 1965 than in 1963 and 1964. If information



RESERVOIR CONDITIONS

Period	April 18 - May 22, 1964
Pool status	Sustained 44 ft. level
Pool level	43.85
Inflow	25,837 c.f.s.
Spill discharge	15,199 c.f.s.
Total discharge	26,511 c.f.s.

FIGURE 6. Direction (per cent of time) and average velocity (f.p.s.) of currents recorded at 10-foot depth in Brownlee Reservoir during period of sustained -44 foot level with spill; April 18 to May 22, 1964. Direction of current reads toward point of wedge.

presented by Brett (1952), Ellis (1944), and Ferguson (1958) is applicable to Brownlee Reservoir, then temperatures and oxygen concentrations during August and September in all years were marginal for survival of salmonids. Carbon dioxide, silicates, sulfates, pH,

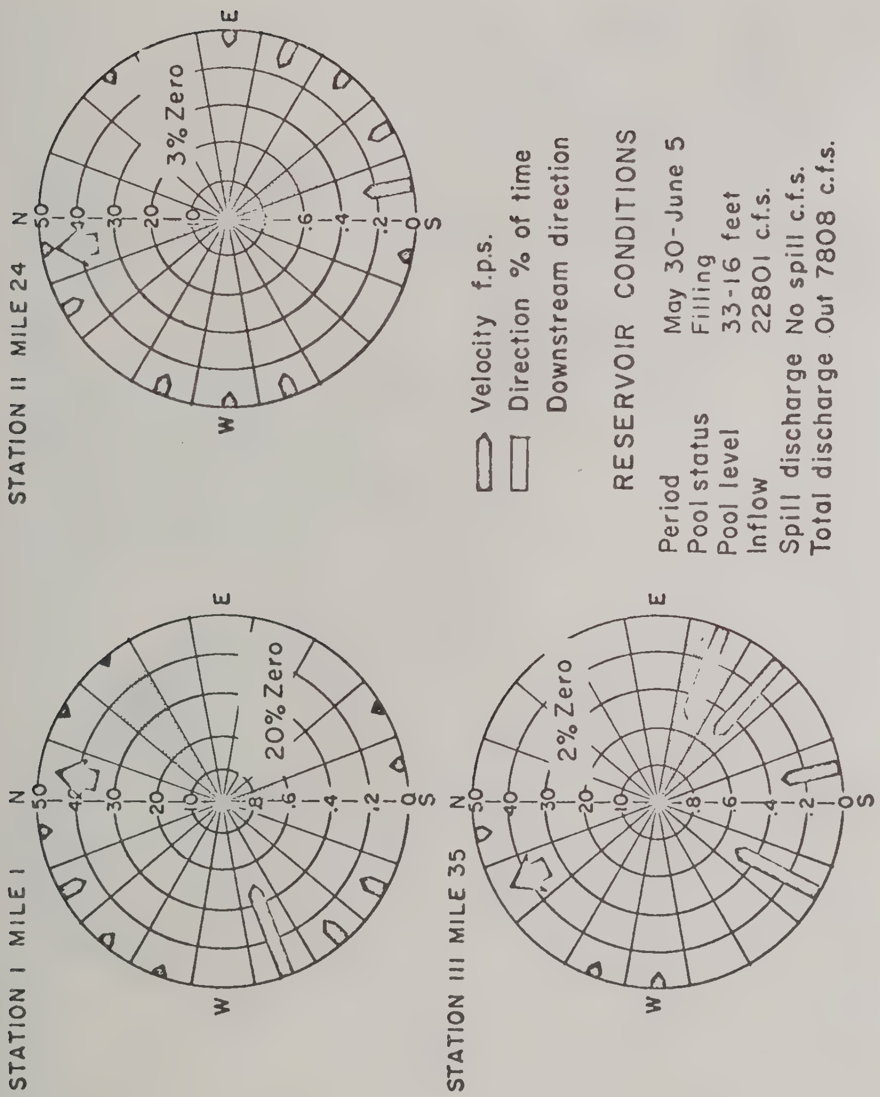


FIGURE 7. Direction (per cent of time) and velocity (f.p.s.) of currents recorded at 10-foot depth in Brownlee Reservoir during a period of filling with no spill; May 30 to June 5, 1964. Direction of current reads toward the point of wedge.

conductivity, alkalinity, and turbidity were within acceptable limits for fish, although in some areas of the reservoir conductivity and pH did reach near-critical values (9.0 pH and 1,000 mhos; Ellis, 1944) at times.

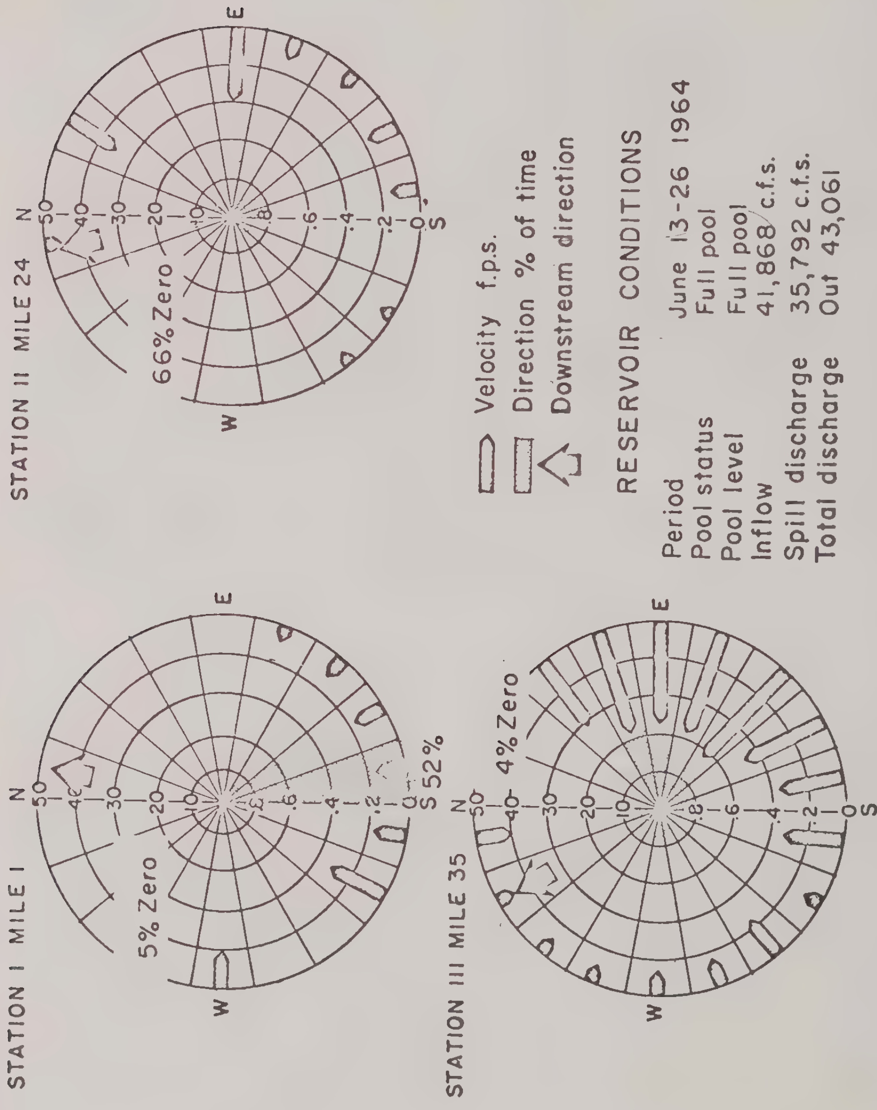


FIGURE 8. Direction (per cent of time) and velocity (f.p.s.) of currents recorded at 10-foot depth in Brownlee Reservoir during a period of full pool with spill; June 13-26, 1964. Direction of current reads toward center of wedge.

SURVIVAL AND SPAWNING OF ADULTS

The Bureau of Commercial Fisheries conducted a study at Brownlee Reservoir in 1962 to determine the effect of a large impoundment on spawning migrations of chinook salmon. The Idaho Department of Fish and Game did similar research in 1960 and 1961.

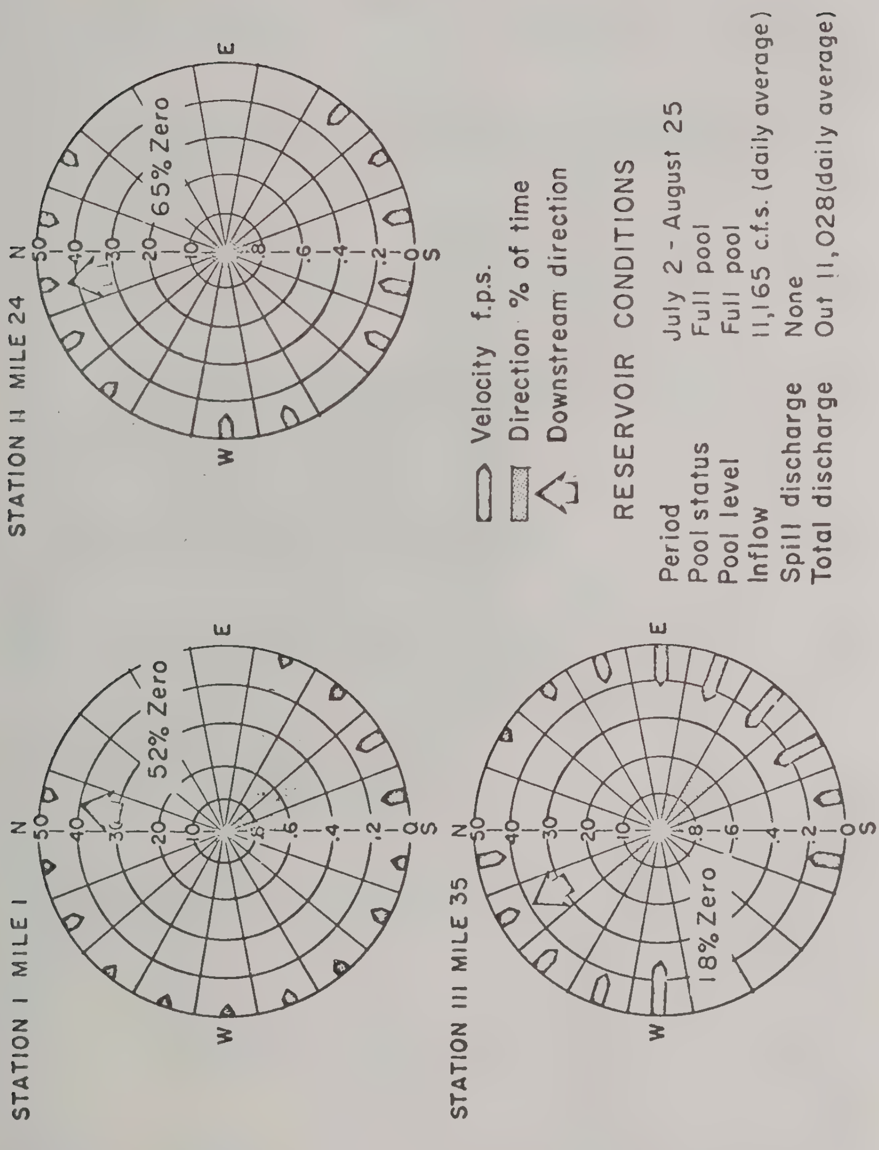


FIGURE 9. Direction (per cent of time) and velocity (f.p.s.) of currents recorded at 10-foot depth in Brownlee Reservoir during period of full pool with no spill; July 2 to August 25, 1964. Direction of current reads toward point of wedge.

Part of the fall run captured by the fish trap below Oxbow Dam (Figure 1) in 1962 was divided into four groups and handled as follows: group 1—disc-tagged, transported around the reservoir, and released in the Snake River about 10 miles above the reservoir; group

2—disc-tagged, transported, and released in the lower portion of Brownlee Reservoir; group 3 (controls)—handled least, transported, released in the lower reservoir like group 2; and group 4—fin-clipped (adipose), handled like the tagged groups, transported, and released in the lower reservoir like groups 2 and 3.

All four groups were treated with 1 ppm Malachite Green during the first hour of transport. The tagged and fin-clipped fish were also anesthetized before handling and their wounds treated with either iodine or a 15 per cent solution of Malachite Green; iodine treatment was discontinued early in the study because skin discoloration and formation of blisters. After each day's transport, the truck tanks were sterilized with roccal. This practice was also discontinued when toxic material, left because of improper flushing of a tank, caused a load of fish to die. Malachite Green was substituted thereafter.

When few chinook salmon were migrating, alternate groups were marked and transported each day. Two trucks were used during the peak of migration, however, and releases from all four groups often were made on the same day. Fifty-nine fish were also tagged with sonic tags and released at the upriver site to check on possible "fallback" into the reservoir. Records from monitoring stations on shore and from a portable hydrosonic receiver operated from a boat confirmed that fish released in the river did not fall back but quickly oriented and proceeded upstream to the spawning area.

Tag recoveries from the spawning grounds were compared between years and groups (Table 1). In addition, salmon carcasses were ex-

Table. 1. Recoveries of tagged and untagged chinook salmon on the spawning grounds, 1960-62[1]

Year and release site	Treatment[2]	Number released	Number recovered	Percentage recovered
1960				
Reservoir	Tagged	361	23	6.5
Reservoir	Untagged	4,282	218	5.1
River	Tagged	267	16	6.0
1961				
Reservoir	Tagged	686	70	10.2
Reservoir	Untagged	3,272	467	14.3
River	Tagged	688	83	12.1
1962				
Reservoir	Tagged	444	13	2.9
Reservoir	Fin-clipped	365	31	8.5
Reservoir	Untagged	342	85	24.9
River	Tagged	340	11	3.2

[1] From Trefethen, P. S., and D. F. Sutherland, Passage of chinook salmon (*Oncorhynchus tshawtscha*) through a large impoundment. Bureau of Commercial Fisheries, unpublished manuscript.

[2] In 1960 the largest and healthiest fish were selected for tagging (Hauk, 1961). In 1961 fish were randomly assigned to each group (Graban, 1964). In 1962 the hatchery selected some of the largest and healthiest fish. The remainder were assigned to either a tagging group or the fin-clipped group. The untagged group in 1962 included fish taken directly from the fish trap and handled as little as possible before release.

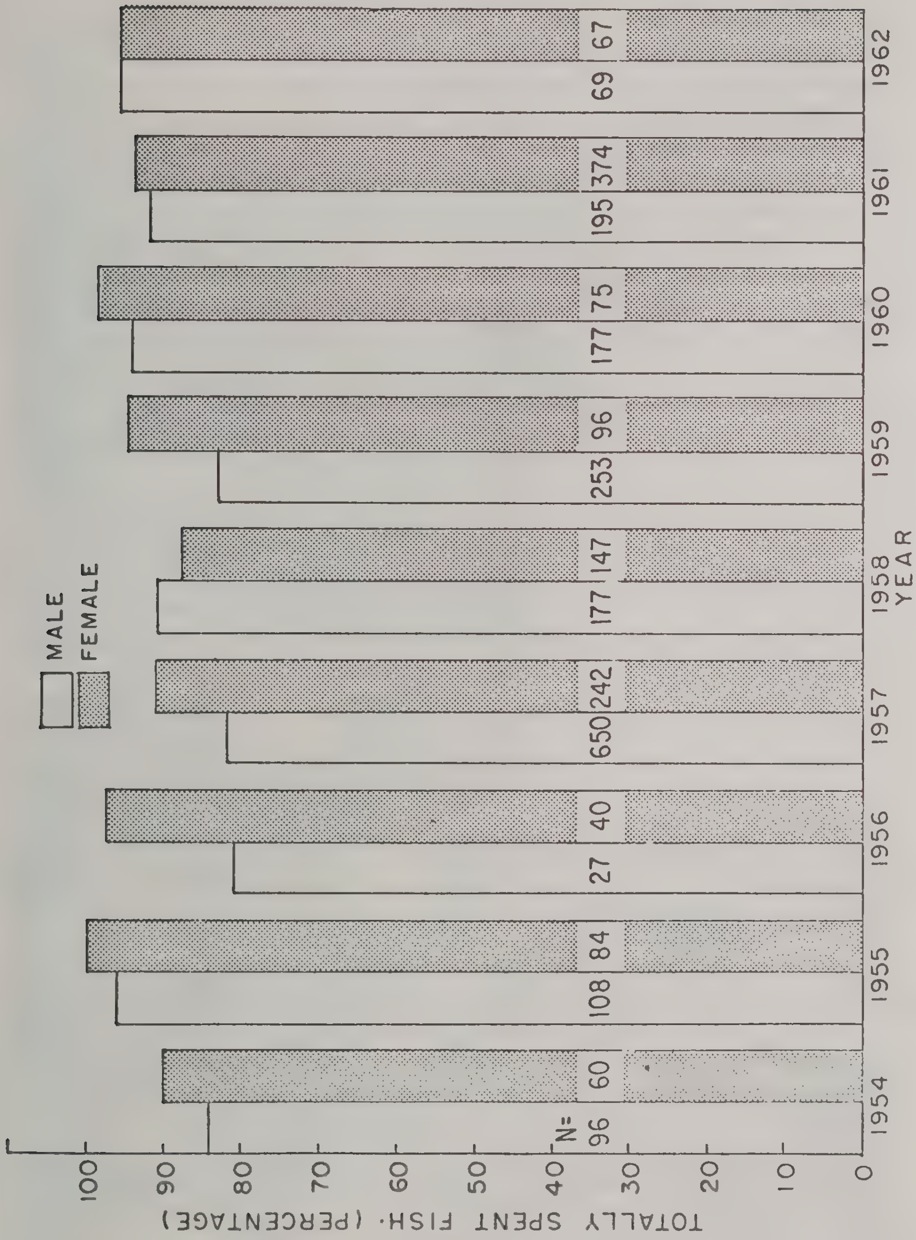


FIGURE 10. Percentage of totally spent fall-run chinook salmon recovered on spawning ground surveys in the Swan Falls area, Snake River. (From Trefethen and Sutherland, 1966, Bureau of Commercial Fisheries, unpublished manuscript. Brownlee Dam was completed in 1958.)

amined for completeness of spawning for comparison with similar data collected from this population before Brownlee Dam was built in 1958 (Figure 10).

No tagged fish were recovered in 1962 from 181 released during the first 4 weeks of tagging (August 27 to September 23), and only 5 were recovered from the 120 tagged during the following 6 days. The stress of tagging and high temperatures at the release sites very likely contributed to this early loss of tagged fish.

Two significant findings emerged from the study. First, chinook salmon that migrated through the reservoir evidently reached the spawning grounds as successfully as those transported around it. Tag recoveries for both groups were low but closely similar each year. Second, inspection of gonads and egg counts from carcasses indicated that spawning was as successful after construction of the dam as before construction.

RECRUITMENT OF JUVENILE SALMON INTO THE RESERVOIR

Studies in 1961 and 1962 indicated that only three streams—Eagle Creek, Snake River, and Weiser River—were being used for spawning by anadromous salmonids. Other systems contributed little to recruitment of juvenile anadromous salmonids into the reservoir.

On the basis of this information it was possible to select two sampling sites from which the entire recruitment to the reservoir could be monitored. A floating modified "migrant dipper trap" (Mason, 1966) with louver leads was installed in the Snake River 5 miles below the mouth of the Weiser River to collect juveniles from spawning areas in the Snake and Weiser rivers; a stationary louver device (Bates and Vinsonhaler, 1957) was used to collect downstream migrants in Eagle Creek near its confluence with the Powder River (Figure 11). Both devices only sampled the downstream migrations; total recruitments were estimated from recapture of marked individuals that had been released upstream.

Snake River and Weiser River populations

Adult chinook salmon of the spring run spawn in the Weiser River from late August through early October. The fry emerge in early spring, spend 1 year in the tributary, and begin their seaward migration in early April as age-group I juveniles. Adults of the fall run spawn in October and November in the main stem of the Snake River. The fry emerge in early spring and smolts of age-group 0 begin to move downstream in late April of their first year of life. As shown in Figure 12 for 1963, both migrations peak at the Snake River sampling site near mid-May and are almost complete by mid-June.

The presence of Brownlee Dam, which had inadequate fish passage facilities, reduced the number of chinook salmon that returned to the spawning grounds. It became necessary to supplement and finally to supplant the indigenous Snake River population with hatchery fingerlings. The success of juveniles of other salmonid species in passing through a large reservoir such as Brownlee was also of interest. In mid-March 1964, 250,000 fall chinook salmon of age-group 0 and

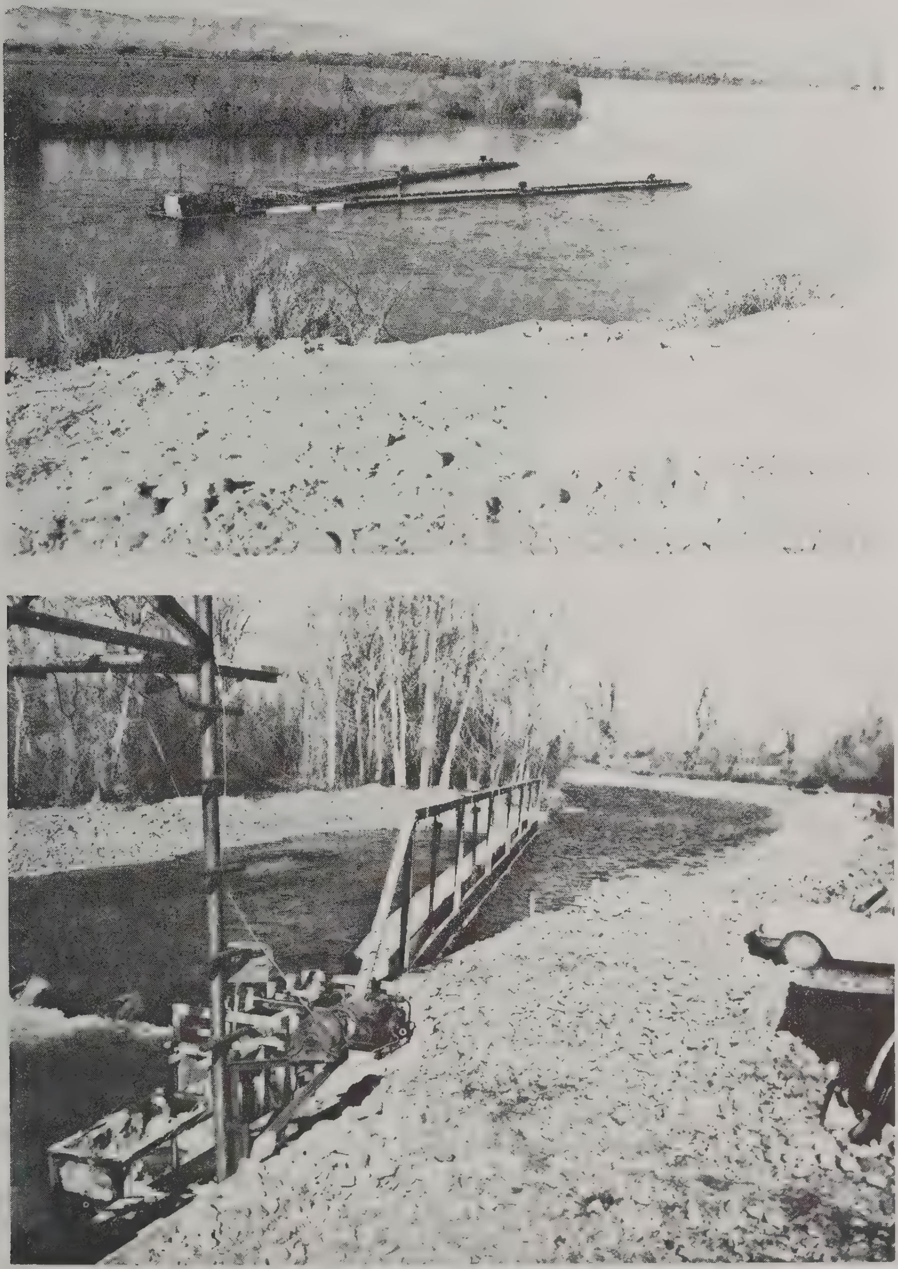


FIGURE 11. Migrant dipper trap fishing at recruitment site on the Snake River near Weiser, Idaho, and the Eagle Creek louver fishing at recruitment site near Richland, Oregon.

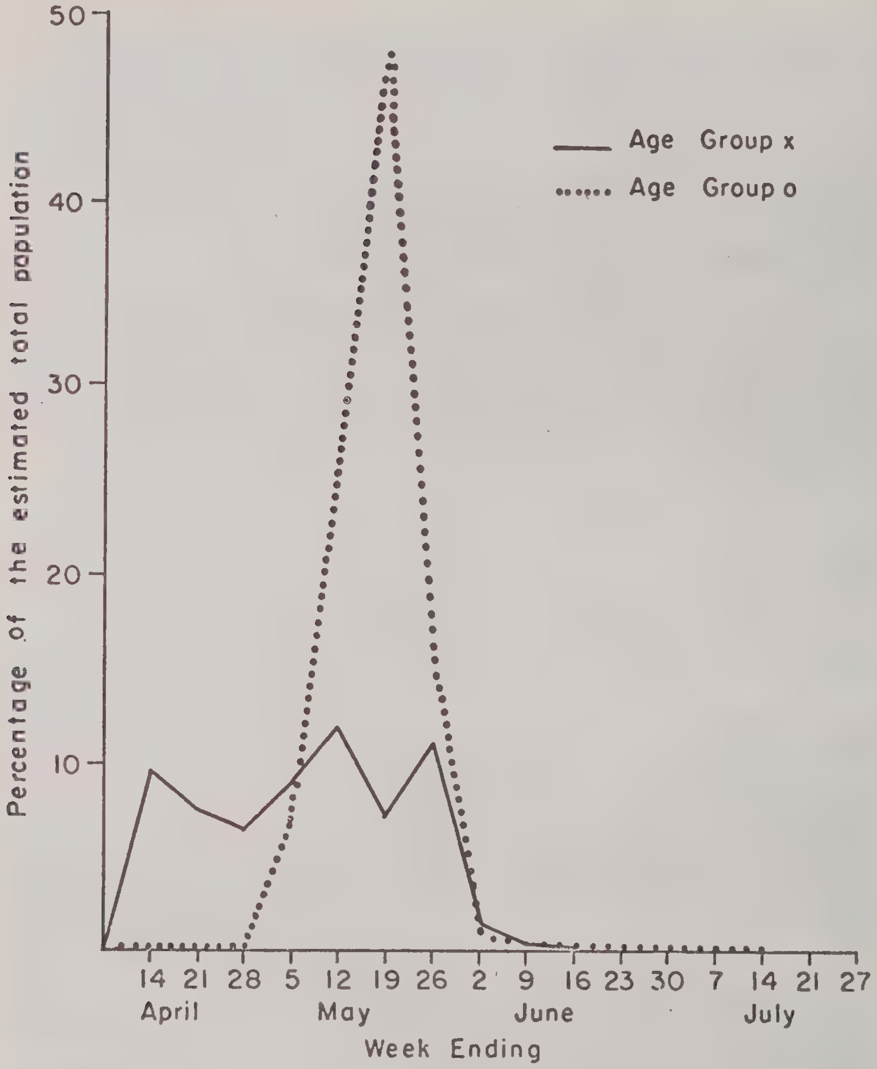


FIGURE 12. Timing of the 1963 Snake River juvenile chinook salmon migration. (From Krcma, Richard F., 1966, unpublished manuscript, Bureau of Commercial Fisheries.)

375,000 coho salmon of age-group I were released in the Snake River about 70 miles above the reservoir. From mid-March through early April 1965, 592,000 chinook salmon of age-group 0 and 473,000 sockeye salmon of age-group I were released about 60 miles above the reservoir.

Eagle Creek population

Spring-run chinook salmon spawn in Eagle Creek at about the same time as in the Weiser River, but downstream migration of juveniles into the reservoir is much different. Peak emigration from Eagle

Creek coincides with increased water flows during fall; a much smaller secondary peak occurs just before runoff in late spring.

Recruitment to Brownlee Reservoir from the Eagle Creek population is nearly continuous. Fish of age-group I dominate the small migration early in the year, but a few smolts of age-group II are also present. By late April, those of age-group 0 begin to appear in the catches. Age-group II disappears by early summer and proportions of age groups I and 0 decrease and increase, respectively. Few chinook salmon of any age are present at the sampling site during summer and early fall; flows are then very low because considerable water is diverted at upstream locations for irrigation. Most migration past the Eagle Creek louver is between early October and late November when flows are increasing. About 97 per cent are then of age-group 0 and 3 per cent are of age-group I. As we show later, downstream escapement from the reservoir of these juveniles from Eagle Creek is at the same time as that of juveniles from the Weiser and Snake rivers.

MIGRATION OF JUVENILE SALMON THROUGH THE RESERVOIR

As the young salmonids entered the reservoir, individuals were captured, weighed, measured, marked with jab tags and thread tags, and released. Subsequent recapture of marked and unmarked individuals by use of floating traps, surface and mid-water trawls, purse seines, and gill nets yielded information on rates and direction of migration, growth, and spatial distribution of the young fish. This information and data collected on the reservoir environment were used to assess the effect of the reservoir on the migrations of anadromous fish.

The recruitments, escapements, survival, and seasonal peaks of migration for all species and populations were estimated for the years 1963-65 (Table 2). Variability in trap catches and the low recovery of marked fish during the beginning and end of the recruitment migration required the use of a "conservative" method of estimating recruitment in order not to over-emphasize the effect of the reservoir on survival during passage. Seasonal average tag returns were used to correct estimates for periods when no tag returns were available. These averages were larger than those during the weeks immediately following the period when no-return data were available. This method of estimating recruitment no doubt accounts for the discrepancy between recruitment and escapement estimates of 1965.

Snake River and Weiser River populations

In 1963, chinook salmon of age-group I began to enter the reservoir from the Weiser River in significant numbers during late April and early May. Intermingled with these fish were chinook salmon of age-group 0 from the Snake River, but juveniles from the Snake River appeared 2 weeks later than those from the Weiser River.

By early May the reservoir was full and warming; colder water of

Table 2. Estimated recruitments, escapements, survival, and peaks of migration of juvenile salmon through Brownlee Reservoir

Year of migration and salmon population	Estimated recruitment[1]	Peak recruitment	Estimated escapement	Peak escapement	Percentage survival
1963					
Snake River chinook	374,500	Mid-May	52,100	Late June	13.9
Weiser River chinook	15,000	Late April	5,900[3]	Mid-May	17.0
Eagle Creek chinook	19,736	Mid-April			
1964					
Snake River chinook	111,500[2]	Mid-May	94,500	Late May	84.7
Weiser River chinook	6,800	Late April	7,200[3]	Late April	51.3
Eagle Creek chinook	7,226	Late April			
1965					
Snake River chinook	162,800[2]	Early May	275,200	—	169.0
Weiser River chinook	3,200	Late April	Too few to distinguish stock	—	—
Eagle Creek chinook	97	Early January			
1964					
Snake River coho[4]	69,000	Early May	51,600	Mid-May	74.78
1965					
Snake River sockeye[4]	360,000	Early April	408,100	Early April	113.4

[1] A "conservative" method of estimate was used for all years. (See text for explanation.)

[2] Includes both native and hatchery stock.

[3] Escapement estimates for Eagle Creek and Weiser River combined.

[4] Hatchery stocks released in Snake River.

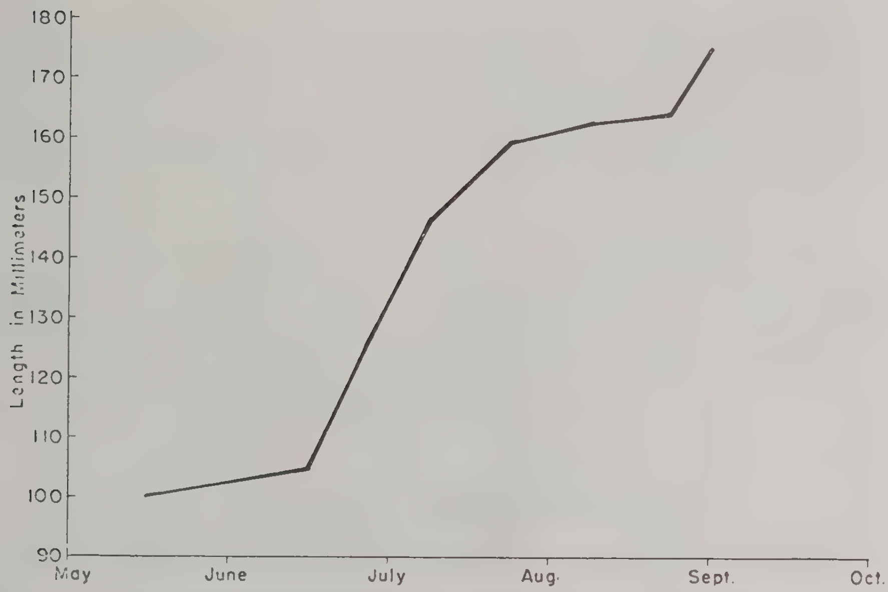


FIGURE 13. Mean length of juvenile salmon sampled in Brownlee Reservoir, 1965. (Preliminary computations from unpublished data provided by Mr. Joseph T. Durkin, project leader of Bureau of Commercial Fisheries fingerling behavior studies, Brownlee Reservoir.)

the Snake River began to form a density layer beneath the surface which soon caused a rather sharp convergence line to appear at the upper end of the reservoir. Most juveniles remained upstream in the river water of the reservoir surface until the convergence line disappeared in late June. Escapement data indicated that the larger and older Weiser River fish, with their slightly earlier peak of migration, were least affected by these conditions (Table 2). Rapidly deteriorating physical conditions, however, had a decided effect upon the later migrants—primarily Snake River fish of age-group 0.

By late June and early July, reservoir surface temperatures were in the low 70's (F) and oxygen depletion was proceeding upward from the bottom. These conditions were especially prevalent in the upper end of the reservoir (Figure 2). Increasing surface temperatures and decreasing dissolved oxygen later forced the remaining juveniles into restricted and marginal habitats (Figures 2 and 3). By late September and October, the physical conditions of the reservoir began to moderate, and the remaining young salmon began to disperse throughout the reservoir. Juvenile salmonids grew rapidly except during the critical months of August and September, when growth rate slowed and a check developed on the scales of the juveniles that remained in the reservoir (Figure 13). Those groups that did not complete their migration through the reservoir in the spring of the first year suffered a high mortality in the reservoir.

Eagle Creek population

As previously noted, recruitment from Eagle Creek is highest during fall when reservoir conditions are moderating. Recaptures of marked fish indicated that these fish spend winter in the reservoir—primarily in the Powder River Pond and Arm (Figure 1)—and then begin seaward migration in the spring just after the peak from Eagle Creek.

Hatchery stock

A comparison between passage times and survival of hatchery stocks of juvenile coho and chinook salmon released together during 1964 indicates little difference in either their passage times or survival. Juvenile coho salmon peaked at the recruitment and escapement sites about 2 weeks before the chinook salmon, but this difference did not appear to shorten their passage time through the reservoir or increase their survival during passage.

Juvenile chinook (age-group 0) and sockeye salmon (age-group I) reared in a hatchery were released in 1965 above the reservoir from mid-March through early April. The chinook salmon delayed their migration downstream and did not peak at the recruitment site until

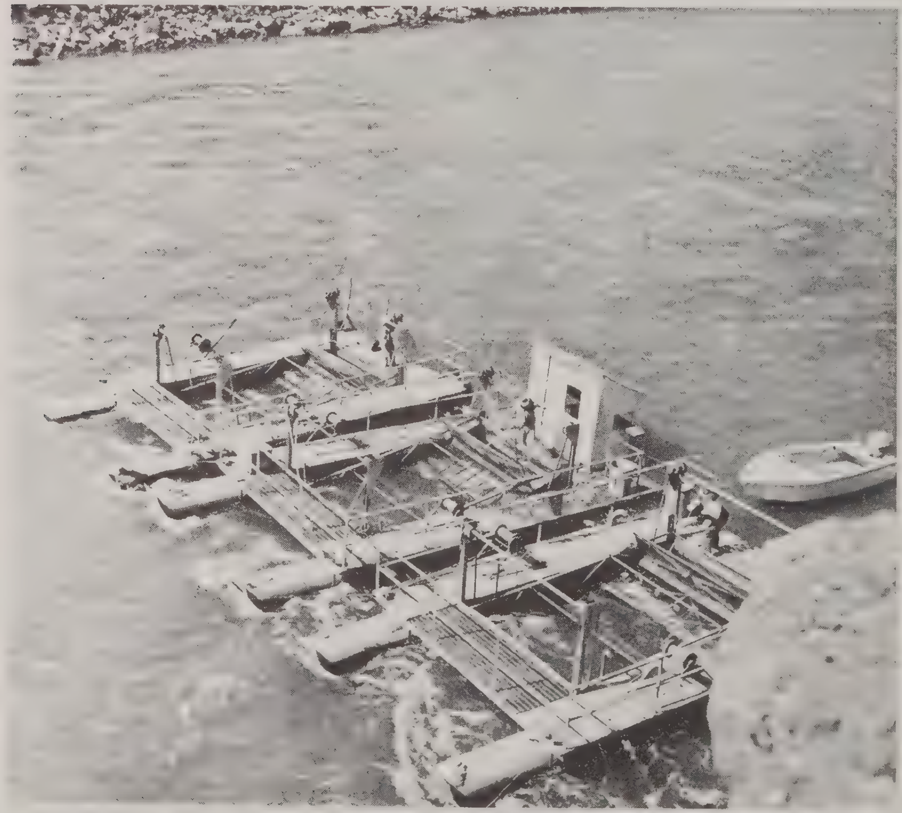


FIGURE 14. Scoop traps shown fishing in tailrace below turbines at Brownlee Dam.

nearly a month after release; by contrast, the juvenile sockeye salmon peaked at the recruitment site about 2 weeks after the first releases. Even though the main portion of these groups arrived at Brownlee Reservoir nearly 1 month apart (sockeye salmon in early April, chinook salmon in early May), they did not differ greatly in survival through the reservoir (Table 2); similar drawdown and currents in both April and May of 1965 may account for this agreement. Early migration may aid survival during passage through the reservoir in most years—when operation typically consists of a drawdown of about 50 feet followed by a filling period that brings the reservoir to full pool by early May. Thus, an early migrant would pass through the reservoir during drawdown when currents are well oriented downstream and the reservoir is relatively short.

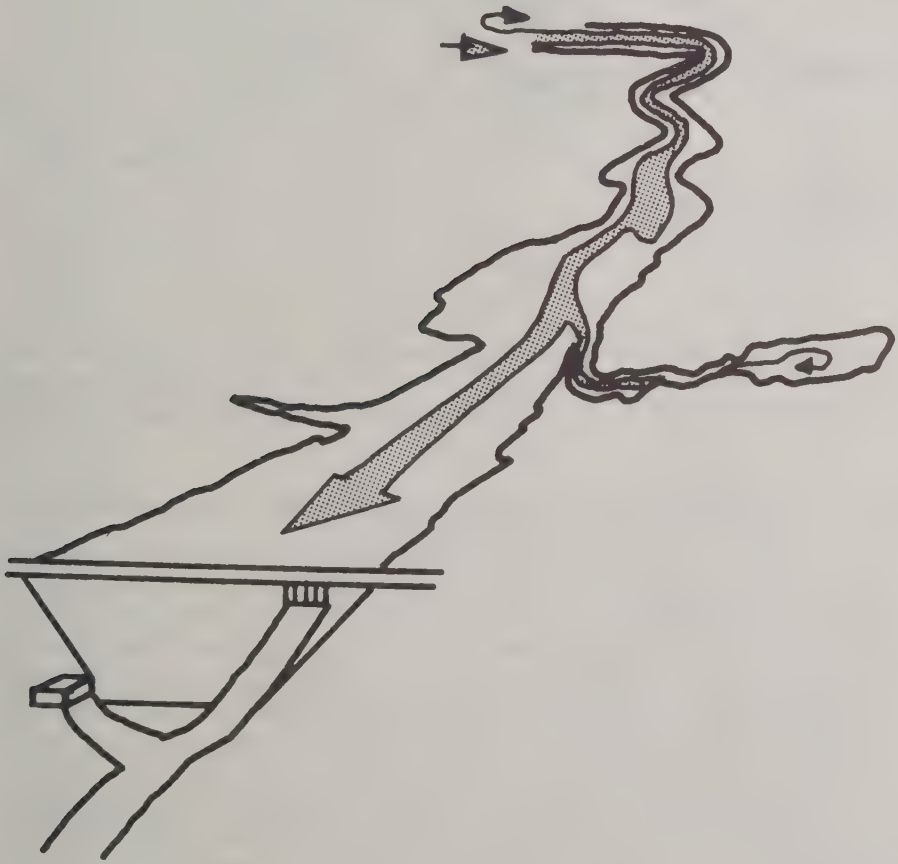


FIGURE 15. Indicated direction of movement of Age O Snake River fall chinook salmon in Brownlee Reservoir during 1963. (From Durkin, Joseph T., 1966, unpublished manuscript, Bureau of Commercial Fisheries.)

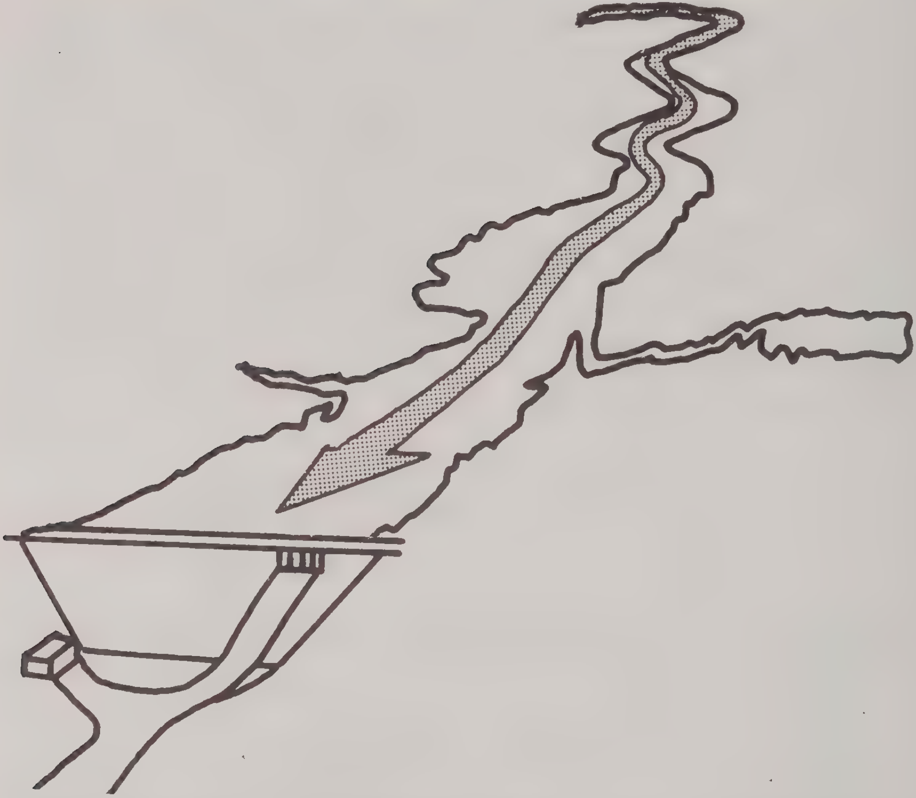


FIGURE 16. Indicated direction of movement of Age O Snake River fall chinook salmon (hatchery stock) in Brownlee Reservoir during 1965. (From Durkin, Joseph T., 1966, unpublished manuscript, Bureau of Commercial Fisheries.)

ESCAPEMENT OF JUVENILE SALMON FROM THE RESERVOIR

Young salmon leaving Brownlee Reservoir either passed through the turbine penstocks, over the spillway (when in operation), or through a skimmer-net collection system for juvenile fish near the forebay of the dam. (The skimmer net was partially dismantled in the fall of 1963 and removed in the summer of 1964.) Escapement of juveniles from the reservoir was assessed by catches in scoop traps in the river below the dam (Figure 14). Trap efficiencies were estimated by recapture of marked fish released through the turbines and in the spillway.

Annual changes in pool level cause changes in reservoir length, current orientation, and velocity. From the combined data from environmental and escapement studies (Table 2), we find that escapement was poor (14-17 per cent) in 1963 when the reservoir was full and currents were disoriented (frequently other than downstream) and of very low velocity. Escapement in 1964 was intermediate (51-58 per cent) at intermediate conditions, and excellent (100 per cent in-

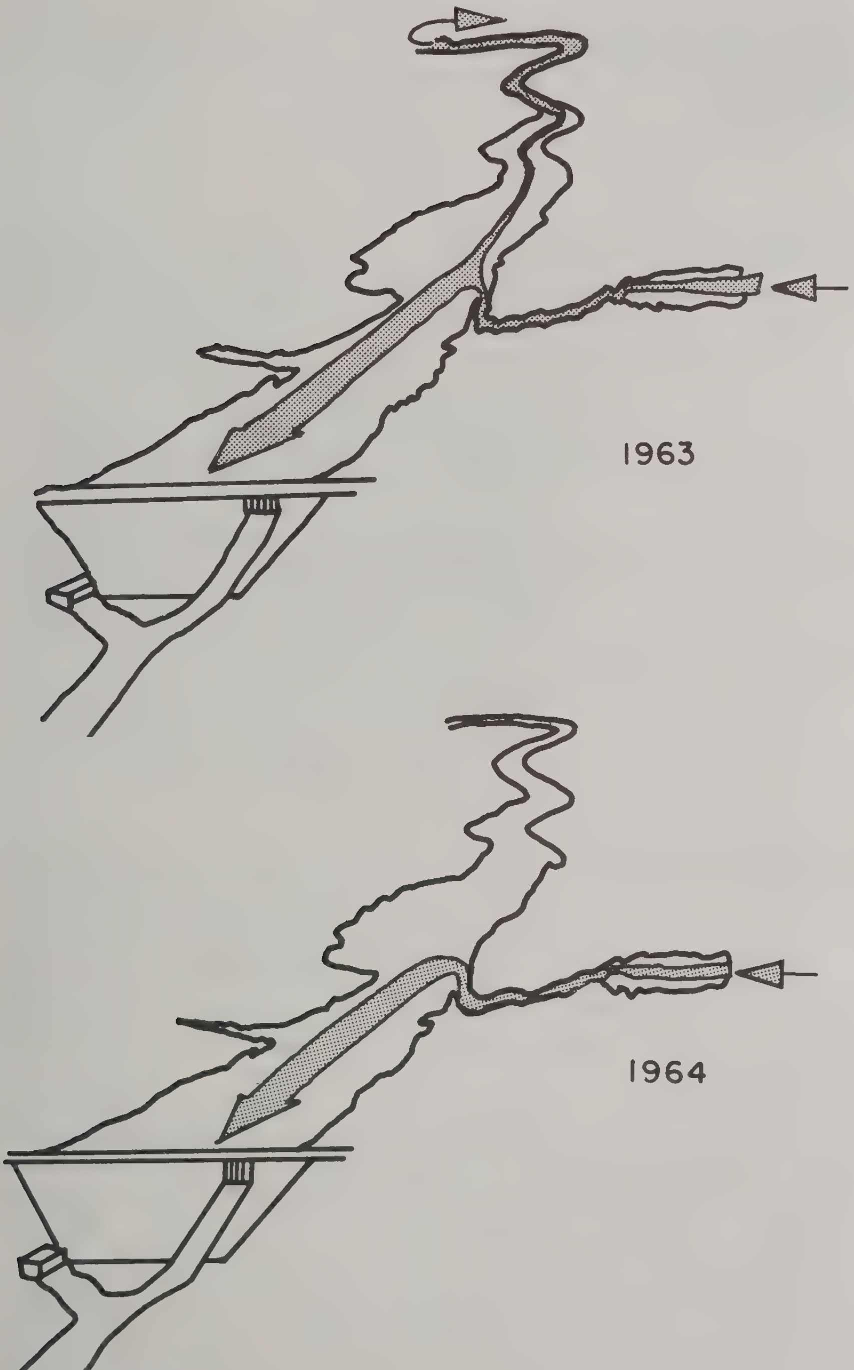


FIGURE 17. Indicated direction of movement of Eagle Creek chinook through Brownlee Reservoir during 1963 and 1964. (From Durkin, Joseph T., 1966, unpublished manuscript, Bureau of Commercial Fisheries.)

dicated) in 1965 which saw a large drawdown, minimum reservoir length, and well-oriented downstream currents. These data are verified by the migration displayed by tagged fish for the 3 years (Figures 15, 16, and 17).

CONCLUSION

1. Passage and spawning of adults
   a. Although the studies on adult chinook salmon were handicapped by an apparent severe loss of tagged fish, they indicated that adults were able to pass through Brownlee Reservoir and reach the spawning ground as well as those transported around it.
   b. As assessed by percentages of spent fish examined, adults that reached the spawning ground after construction of Brownlee Dam in 1958 appeared to have spawned as successfully as those reaching the spawning grounds before the reservoir was present.
   c. The reservoir affects temperature and dissolved oxygen concentrations in the Snake River below the dam. River temperatures below Brownlee Dam averaged 62 F in October, or about 9 F higher than in the river above the reservoir. Dissolved oxygen concentrations, however, averaged 3.6 ppm below the dam or about 5 ppm less than in the river above the reservoir. These conditions may place additional stress on migrating adult salmon during the fall. A reversal of these trends in early summer could benefit migrations of adult salmon in the spring and early summer.
2. Passage of juveniles
   a. Escapement of juveniles from the reservoir was least successful in 1963 when the reservoir was full and when currents were random and slow. Escapement was intermediate in 1964 when drawdown was moderate and downstream flow more pronounced. The best escapement (almost 100 per cent) was in 1965 when drawdown was large and the reservoir current was well oriented downstream.
   b. The importance of reservoir currents on the success of escapement of juvenile salmon from the reservoir was further substantiated by migration patterns of tagged fish within the reservoir. Upreservoir movement of fish was greatest in 1963 when reservoir currents were frequently disoriented and velocities were low.
   c. Mortality was high among juvenile salmonids that did not complete their migration through the reservoir in the spring of the year after entry. Juveniles still in the reservoir in August and September were restricted to marginal habitats between zones of high temperature in the epilimnion and a low oxygen content in the hypolimnion. Variability in trap catches and low recovery

of marked fish at the beginning and end of the recruitment migration necessitated making "conservative" estimates of recruitment in order not to over-emphasize the effect of the reservoir on success of passage. This procedure and the large annual changes in reservoir conditions tended to mask differences between species negotiating the reservoir. The stock of hatchery sockeye salmon used in 1965, however, appeared to have the shortest and most compact migration through the reservoir for any year, species, or source of fish. Early and short migration may improve survival during the average year when reservoir drawdown is moderate (-50 feet) and filling is complete by mid-May.

Acknowledgments

We thank Messrs. Joseph T. Durkin, Donn F. Park, Richard F. Krcma, Carl W. Sims, and Parker S. Trefethan of the Fish-Passage Research Program, Bureau of Commercial Fisheries, for providing data and figures from their unpublished manuscripts for use in this paper. Mr. Durkin provided Figures 15, 16, and 17; Mr. Krcma provided Figure 12, and Mr. Trefethan provided Figure 10. We also thank Mr. Wendell Smith of the Idaho Power Company, and personnel of the Idaho State Department of Fish and Game for their cooperation and help during the study.

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Diurnal Fluctuations in Censuses of Migrating California Gray Whales

by
DONALD H. RAMSEY
Division of Natural Sciences
University of California
Santa Cruz, California
and
Marine Mammal Biological Laboratory
U.S. Fish and Wildlife Service
Seattle, Washington

Each autumn California gray whales, *Eschrichtius gibbosus,* leave their feeding grounds in the Bering and Chukchi Seas to migrate southward toward lagoons in Baja California where they calve and breed. Their migratory route south of Vancouver Island generally lies in shallow water within a few miles of the coast (Norris, 1967) and observers on shore can estimate the size of the population by counting passing animals.

While participating in a gray whale census during 1967—68 at Point Loma, San Diego County, California, I observed a diurnal fluctuation in the number of whales sighted: significantly fewer passed the counting station in the middle of the day than during the early morning or evening. Other investigators (Gilmore, 1960; Rice, 1961; Hubbs and Hubbs, 1967; Adams, 1968) have assumed that the whales migrate southward at a steady rate throughout the day. Population estimates have usually been based on extrapolations of the observed rate during periods of good visibility over those periods when the whales could not be seen. This paper analyzes hourly fluctuations in counts made during the 1954—55 (Gilmore, 1960) and 1967—68 censuses at Point Loma and compares them to the 1967—68 census at Yankee Point, Monterey County, California.

At the Point Loma counting station observers maintained a daily watch from 0700—1700 hours, 27 December 1967 to 16 February 1968. This watch was divided into two five-hour shifts to facilitate observational accuracy. The number of whales in each pod were counted by carefully observing, with binoculars, the location and sequence of blows.

The numbers of whales counted during hourly periods throughout the 1967—68 census at Point Loma were added together (Fig. 1, Table 1). A chi-square goodness

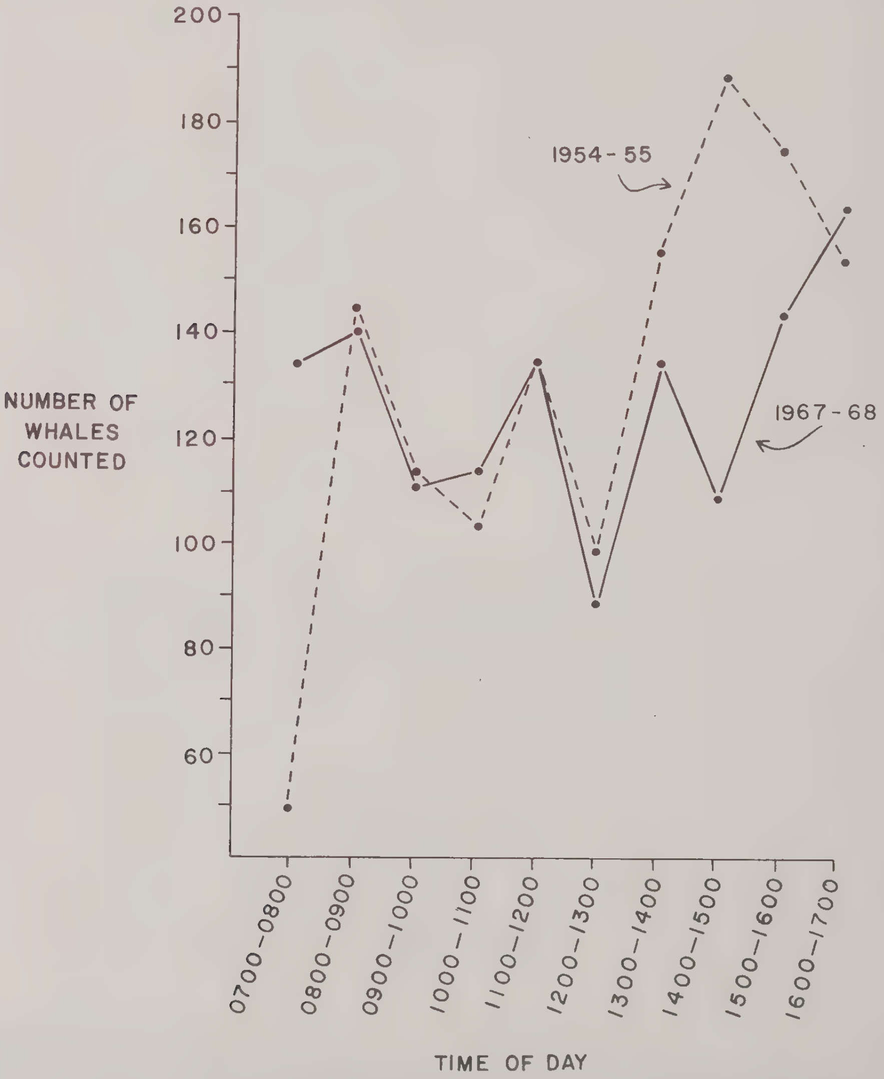

Fig. 1. Numbers of gray whales seen during hourly periods throughout the census period at Point Loma, California during censuses in 1954—55 (Gilmore, 1960) and 1967—68.

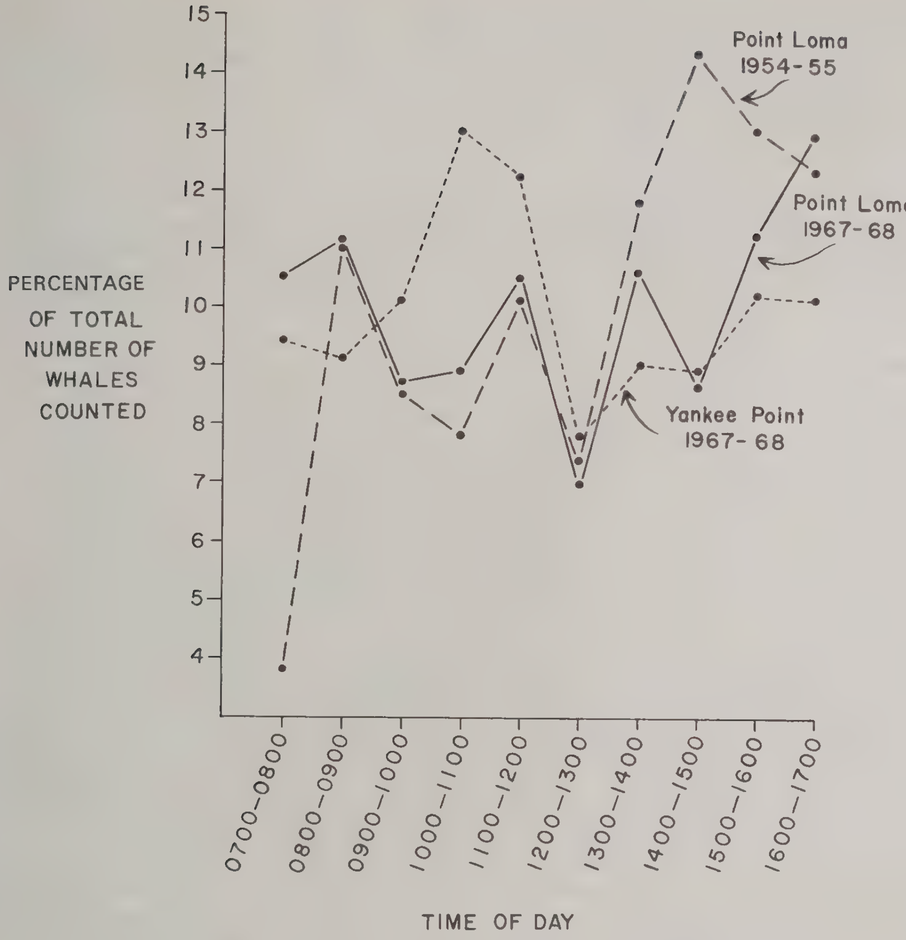

Fig. 2. Percentages of the total number of whales counted at Point Loma in 1954—55 (Gilmore, 1960) and 1967—68, and at Yankee Point in 1967—68 during hourly periods throughout the season.

of fit test shows that these sums fluctuate significantly ($p. < .005$). Confidence intervals for the four hours in the middle of the observation period, 1000—1300 hours, and the first and last two hours, 0700—0900 and 1500—1700 hours, show that there was a significant dip at midday ($p. < .05$). These tests and estimates suggest that there were significantly fewer whales seen in the middle of the day than in the morning and evening.

Gilmore (1960) also added together the number of whales seen during hourly periods in the 1954—55 gray whale census at Point Loma (Fig. 1, Table 1) to check for a diurnal fluctuation in the counts. A chi-square contingency test (to evaluate the hypothesis that two multinomials have the same mean) shows that with the exception of two very divergent periods, 0700—0800 and 1400—1500, it is not possible to reject the hypothesis that there is significant association between the 1954—55 and 1967—68 census data.

The results of the 1967—68 census at Yankee Point (Fig. 2, Table 1) also showed a significant diurnal fluctuation ($p < .005$) but do not show the same pattern as the two censuses at Point Loma. Confidence intervals for the Yankee Point data show that there were significantly more whales seen in the first four hours of the morning than in the last four hours of the afternoon ($p < .05$).

The fluctuations at Point Loma might have resulted from sampling errors, or could reflect a diurnal change in the behavior of the whales. Sampling error could result from changes in visibility due to fluctuating light conditions, fog or haze, or from changing conditions of the water's surface, any of which might interfere with accurate censusing. If real, the fluctuations may relate to a circadian

Table 1

Sums, chi-square goodness of fit values, and percentages of the total number of whales seen during hourly periods in the various censuses.

Place and Year		Hour										
		0700—0800	0800—0900	0900—1000	1000—1100	1100—1200	1200—1300	1300—1400	1400—1500	1500—1600	1600—1700	Total
Pt. Loma 1954—55	Sums	50	145	113	103	134	99	156	189	175	155	1319
	chi^2	50.9	1.3	2.7	6.4	0	8.3	4.4	24.6	14.0	4.0	166.6
	%	3.8	11.0	8.5	7.8	10.1	7.4	11.8	14.3	13.0	12.3	
Pt. Loma 1967—68	Sums	133	142	112	114	136	93	136	111	146	169	1292
	chi^2	0.1	1.3	2.2	1.7	0.4	10.0	0.4	2.5	2.2	12.4	32.2
	%	10.5	11.1	8.7	8.9	10.5	7.0	10.6	8.6	11.2	12.9	
Yankee Pt. 1967—68	Sums	283	273	304	391	366	234	271	268	308	304	3002
	chi^2	1.0	2.4	0	27.6	14.5	14.5	2.8	3.4	0.2	0	66.4
	%	9.4	9.1	10.1	13.0	12.2	7.8	9.0	8.9	10.2	10.1	

behavioral rhythm, or changes in behavior due to disturbance by small boat traffic. Gilmore (1960) suggested that the fluctuations in the 1954—55 census were the result of sampling errors. He stated that the high figures for the afternoon were «probably the result of improved visibility — lifting of the haze. The low values at 7 a.m. and noon may (?) represent human errors of some kind.»

To test for a correlation between restrictions in visibility and fluctuations in the census, I added together the number of times during each hourly period in the 1967—68 census when visibility was less than two miles. For the ten periods from 0700—0800 to 1600—1700 these figures were: 14, 12, 10, 11, 11, 14, 14, 13, 14 and 11. A chi-square test indicates that there was no significant variation in the time of occurrence of the periods of restricted visibility and suggests that they were not responsible for the fluctuations.

It is more difficult to eliminate, with available information, the possibility that a diurnal change in the intensity and direction of sunlight is responsible for the fluctuations in the counts. To convincingly test this hypothesis it would be necessary to use other censusing techniques — observations from airplanes or ships — to determine the efficiency of shore observers under varying conditions of light.

In further criticism of Gilmore's (1960) hypothesis, it seems unlikely that the low figures at noon are the result of human error. At noon a fresh observer went on duty and would probably have missed fewer whales than an observer finishing a five-hour watch. It is possible that the low figures for the 1954—55 census from 0700—0800 could result from a lack of punctuality in beginning the count at 0700.

The observations at Point Loma, then, suggest that a diurnal cycle exists in the activity of the whales such as that reported for the Minke whale, *Balaenoptera acutorostrata* (Kimura and Nemoto, 1956) and for pinnipeds (Fiscus et al., 1965). But this hypothesis is difficult to defend in face of the Yankee Point data; one would expect a similar trend at both censusing areas. The effect of small boat traffic can not be evaluated because no record of it was made during the censuses, but there certainly are many fewer boats at Yankee Point than at Point Loma. Hubbs and Hubbs (1967) note that the increase in harassment from small boats in the Point Loma area might well cause gray whales to migrate further offshore. Thus, small boats might be responsible for a fluctuation there, but not at Yankee Point.

Although the causes of diurnal fluctuations are not yet known, the phenomenon must be carefully considered by cetologists estimating the number of gray whales. If the fluctuations result from a behavioral cycle, their effect upon population estimates will vary with the time of day when censuses are made. If the fluctuations are due to technical problems, such as changes in lighting, the effect will vary with the method of observation. The distortion will be greatest when estimates are based on very brief censuses, but the validity of any estimate which omits a correction for diurnal fluctuation may be seriously impaired.

I am grateful to Dr. R. S. Peterson for advice and assistance in the development of this manuscript, and to D. W. Rice who willingly gave access to the gray whale census

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Migration Rates of Yearling Chinook Salmon in Relation to Flows and Impoundments in the Columbia and Snake Rivers

HOWARD L. RAYMOND

Migration Rates of Yearling Chinook Salmon in Relation to Flows and Impoundments in the Columbia and Snake Rivers

HOWARD L. RAYMOND

Bureau of Commercial Fisheries, 2725 Montlake Boulevard East, Seattle, Washington 98102

ABSTRACT

Migration rates of yearling chinook salmon (*Oncorhynchus tshawytscha*) through free-flowing and impounded stretches of the Snake and Columbia Rivers were compared during periods of low and moderate river discharge. Generally, the rate of migration was directly related to the water flows; it was 21 km/day at the low river discharge (Columbia—4,248 m^3/sec; Snake—1,416 m^3/sec), and 37 km/day during moderate river discharge (Columbia—8,495 m^3/sec; Snake—2,265 m^3/sec). Migration rates through most free-flowing and impounded stretches of the Snake and Columbia Rivers were similar with the one exception that in McNary Reservoir (Columbia River) fish moved only about one-third as fast as elsewhere.

Marked yearling chinook salmon from the Salmon River took 32 days to travel the 669 km to Bonneville Dam during the low river discharge in 1966. New impoundments may more than double the travel time now required during low river flows.

INTRODUCTION

The Columbia River has been almost completely transformed from a free-flowing stream to a series of impoundments behind lowhead dams. Similar changes will soon occur on its largest tributary, the Snake River, which is a significant producer of spring and summer-run chinook salmon (*Oncorhynchus tshawytscha*). Juveniles from these runs of salmon must now pass downstream to the sea as yearlings through the impoundments above Ice Harbor Dam on the Snake River and above McNary, The Dalles, and Bonneville Dams on the Columbia River. In the near future these fish will be required to negotiate an additional three to five impoundments on the Snake River and one large impoundment above John Day Dam on the Columbia River before they reach the sea (Figure 1).

For several years, information has been accumulated on the movement and survival of juvenile salmon, in relation to the changing environment in the Columbia Basin. These data revealed that most of the fish presently pass downstream in midspring before the peak river flows in June. Fishery managers are interested in the potential effects of additional impoundments and regulations of flow on movement and survival.

This paper provides estimates of the rate of migration of yearling chinook salmon through impounded and free-flowing sections of the Columbia and Snake Rivers during low and moderate flows. Yearling chinook salmon 90 mm to 130 mm long were studied because they migrate in substantial numbers during both low and moderate river flows; approximately 90%[1] are from the Snake River. The paper also points to the delay in migration that could result from new impoundments.

STUDY AREAS AND MIGRATION RATE CALCULATIONS

Study areas, including free-flowing and impounded sections of the Snake and Columbia Rivers are shown in Figure 1. Table 1 contains data relevant to these study areas.

Migration rates were determined by mark and recapture of specimens. From the beginning of the migration in early April until the end of May 1966, young fish were collected in either scoop traps (in the Salmon River about 84 km above its confluence with the Snake River) or dipnets (specially designed to recover fish from gatewells of turbine intakes at Ice Harbor, McNary, The Dalles, and Bonneville Dams). Methods of collecting, marking, and releasing fish from gatewells was described by Bentley and Raymond (1968). Water temperatures, generally, ranged from near 10 C in early April to 13 C by late May.

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[1] Based on collections of chinook salmon from turbine intake gatewells at Priest Rapids Dam and Ice Harbor Dam, 1965–67. Bur. Comm. Fish., unpublished.

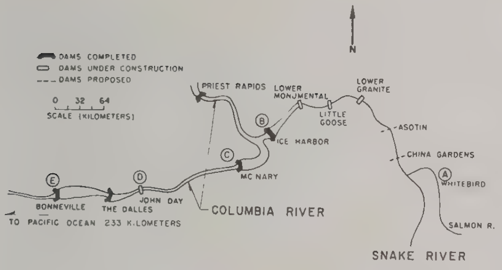

FIGURE 1.—Sites at which marked yearling chinook salmon were released (A, B, C, and D) and recovered (B, C, D, and E) in 1966 to study rates of downstream movement.

Fish were marked with a harmless thermal brand (Groves and Novotny, 1965) and released immediately downstream from sites A through C (Figure 1). Marked fish released at the John Day damsite (D) were obtained from the gatewells of The Dalles Dam and transported to the release site. Fish were not marked at Bonneville Dam (E). Separate marks identified all fish in each weekly release group by release site.

Average time of passage through a specified section of river was determined, for a given group, by subtracting the median date of recovery from the median date of release. The use of the median averted distortion in measurement of central tendency, to which the mean is sensitive. Because fish could not be collected at John Day damsite, migration rates for the 122-km stretch of river from McNary Dam to the John Day damsite were calculated by subtracting the median passage time between the John Day damsite and Bonneville Dam from the median passage time between McNary and Bonneville Dams.

In 1966 enough marked chinook yearlings were recovered to compare migration rates, through separate river sections, of three weekly release groups that had migrated in April, during a low river discharge, with three groups that had migrated in May, during a moderate river discharge. It was assumed that seasonal differences between April and May, in themselves, had no effect on migration rates. This assumption is reasonable, because (1) migration rates of yearling chinook and water flows measured in April 1965 were similar to the migration rates and water flows recorded in May 1966, described later, and (2) the groups of marked yearling chinook salmon compared were of the same size, age, and racial origin.

TABLE 1.—*Average migration rates of yearling chinook salmon through free-flowing and impounded sections of the Snake and Columbia Rivers during low and moderate river discharges*[1]*; data are based on three weekly release groups, each during low and moderate river discharge*

		Low river discharge					Moderate river discharge				
		Number of marked fish		Elapsed time (days)		Migration rate	Number of marked fish		Elapsed time (days)		Migration rate
Stretch of river and type of flow[2]	Distance (km)	Released	Recaptured	Average	Range	(km/day)	Released	Recaptured	Average	Range	(km/day)
Salmon River to Ice Harbor Dam (A–B) (nearly free flowing)	370	16,000	718	14	13–15	26	9,500	103	8	7–9	47
Ice Harbor Dam to McNary Dam (B–C) (impounded)	68	13,000	1,001	9	7–10	8	11,000	164	5	4–6	13
McNary Dam to John Day damsite (C–D) (free flowing)	122	36,400	702	5	5[3]	24	19,000	96	3	2–3	40
John Day damsite to Bonneville Dam (D–E) (impounded)	109	5,500	132	4	3–5	27	4,800	52	2	2[3]	55
Salmon River to Bonneville Dam (A–E) (based on sum of above)	669	—	—	32		21	—	—	18		37
Salmon River to Bonneville Dam (A–E) (based on recovery at Bonneville of fish released in Salmon River)	669	16,000	44	31	29–33	21	9,500	7	19	17–21	35

[1] Low river discharge: Snake 1,416 m³/sec (Ice Harbor Dam); Columbia, 4,248 m³/sec (McNary Dam); moderate river discharge: Snake 2,265 m³/sec (Ice Harbor Dam); Columbia, 8,495 m³/sec (McNary Dam).

[2] See Figure 1 for location of release and recovery sites.

[3] Average number of days between release and recovery was the same for all three replicates.

ESTIMATED MIGRATION RATES

Average migration rates were different during periods of different river discharges (Table 1). At moderate river discharges, the migration rate from the Salmon River to Bonneville Dam was 37 km/day, as compared with the 21 km/day estimated for the low river discharge. Yearling chinook salmon from the Salmon River migrated to Bonneville Dam in 18 days at the higher flow and in 32 days at the lower flow. Estimates based on a summation of recoveries in individual sections of the river agreed closely with those obtained from fish marked at the Salmon River and recovered at Bonneville Dam (Table 1).

The relation between river discharge and migration rate of juvenile salmon was also indicated by a pilot study conducted during April of 1965 to determine the practicability of a major mark and recovery program. Yearling chinook salmon and steelhead trout (*Salmo gairdnerii*) were collected and marked at Ice Harbor Dam and recovered at Bonneville Dam. Although the data could not be compared in detail with those for 1966, the recoveries from 10,000 marked fish released indicated rates of migration similar to those measured in May 1966. The average rate was 37 km/day, during water flows varying between 7,079 and 9,911 m^3/sec, compared to an average of 31 km/day at flows of 8,495 m^3/sec for this section of stream in May 1966.

Migration rates through most free-flowing and impounded stretches of the Snake and Columbia Rivers were similar with one exception; in McNary Reservoir (Columbia River) fish moved only about one-third as fast. This slower movement may have been caused by comparable reduction in water velocity through that section of river. Nelson, Perkins, and Haushild (1966) found that average velocities through McNary Reservoir were between 30 and 42% (depending on discharge) of the average velocity in the Columbia River below McNary Dam. Juvenile salmon from the Snake River may undergo a period of adjustment when they enter the mixture of the Columbia and Snake River waters, which could have accounted for the delay. More likely, however, velocity rather than change in water plays the dominant role in governing movement of fish in this area. In the following discussion on significance of delay, we have therefore assumed that the slowdown of fish through McNary Reservoir was caused by the reduction in water velocity.

SIGNIFICANCE OF DELAY

Although slower movement such as that observed in McNary Reservoir may not now affect the survival of yearling chinook salmon, the cumulative delay caused by a series of impoundments could affect their survival in the future. When John Day Dam, on the Columbia River, and the new dams on the Snake River are completed, the flow dynamics will be vastly changed. The impoundment above John Day Dam (3×10^9 m^3) will be nearly twice that above McNary Dam (1.6×10^9 m^3). Water velocity may be even slower in John Day Reservoir than in McNary Reservoir. The Snake River reservoirs will be smaller than those at McNary and John Day, but flow characteristics may be comparable to those in the larger reservoirs of the Columbia. Impoundments in the Snake River will be only one-third to one-fourth the size of the McNary Reservoir; the average discharge of the Snake River, however, is correspondingly only about one-third of that at McNary Dam, during most of the smolt migration (Table 1). As a result, water velocity in future Snake River impoundments could be comparable to the present velocity in McNary Reservoir.

Migration rates through McNary Reservoir in 1966 averaged 8 km/day during the low river discharge, about one third of the rate calculated through other stretches of river at that time (Table 1). If velocities in future impoundments approximate those in McNary Reservoir, the rate of migration through these impoundments will probably approximate the rate through McNary Reservoir. Yearling chinook required 32 days to migrate from Whitebird on the Salmon River to Bonneville Dam (during lower flows in 1966). If we assume that migration rates down the Snake River (when impounded) will approximate the present rate through McNary Reservoir during low river discharge, yearling chinook from the Salmon and Grande Ronde Rivers will require 36 additional days, or a total of 68 days, to reach Bonneville Dam.

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Stomach Contents and Feeding Behavior of Killer Whales in the Eastern North Pacific

by

Dale W. Rice
Bureau of Commercial Fisheries
Marine Mammal Biological Laboratory
Seattle, Washington 98 115

Abstract: The stomachs of 10 killer whales *(Orcinus orca)* collected in the eastern North Pacific between Kodiak Island, Alaska, and San Miguel Island, California, contained the remains of at least three California sea lions *(Zalophus californianus)*, four Steller sea lions *(Eumetopias jubatus)*; seven elephant seals *(Mirounga angustirostris)*, two harbor porpoises *(Phocoena phocoena)*, two Dall porpoises *(Phocoenoides dalli)*, one minke whale *(Balaenoptera acutorostrata)*, two opah *(Lampris regius)*, one Pacific halibut *(Hippoglossus stenolepis)*, two carcharinid sharks *(?Prionace glauca)*, and one squid. One pod of killer whales harassed a bull California sea lion for 45 minutes before killing it; one killer whale in another pod repeatedly dove and surfaced for 15 minutes with the carcass of a young California sea lion in its jaws.

Although the feeding habits of the killer whale *(Orcinus orca)* are well known by reputation, factual data based on stomach analyses are extremely scarce. Since 1960, staff members of the Marine Mammal Biological Laboratory (MMBL) of the Bureau of Commercial Fisheries have been collecting and examining killer whales and recording observations of this species at sea whenever the opportunity arose during other marine mammal investigations.

We have examined the stomachs of 10 killer whales collected between Kodiak Island, Alaska, and San Miguel Island, California. Five were taken by catcher boats operating from the whaling stations of the Del Monte Fishing Company and the Golden Gate Fishing Company in Richmond, California; three were taken during pelagic fur seal investigations by the MMBL; and two were taken during MMBL whale marking cruises on chartered whale catcher boats.

The only extensive published data on the food of killer whales is the account by Nishiwaki and Handa (1958) of the stomach contents of 364 whales killed in waters adjacent to Japan, based on records submitted by shore whaling stations. Zenkovich's (1938) report on two killer whales taken in the Bering Sea by Soviet whalers appears to be the only other published paper on stomach contents of North Pacific killer whales.

The frequently repeated report that two killer whales taken near the Pribilof Islands had a large number of northern fur seals *(Callorhinus ursinus)* in their stomachs is false, as Jordan (1898: pt. 2, p. 506) pointed out long ago. I know of no documented finds of northern fur seals in killer whale stomachs.

Acknowledgments. — — The following MMBL biologists collected or examined some of the whales: Kenneth Balcomb, James Ekberg, Clifford Fiscus, Bernard Lenheim, Frank Maurer, Thomas McIntyre, Karl Niggol, and Richard Stroud. David Caldwell, of the Los Angeles County Museum, and Clifford Fiscus aided in the identification of the stomach contents, John Caito and Charles Caito, of the Del Monte Fishing Company, and Robert Casebeer, of the Golden Gate Fishing Company, made available to us the killer whales brought into their whaling stations.

Stomach Contents

The collection data and stomach contents of each of the 10 whales are listed below. The stomach contents were identified by comparison with material in the reference collection at the MMBL. The number of individuals listed for each prey species is the minimum necessary to account for the identifiable remains in the stomach; more individuals may have been represented. The data are summarized in table 1.

Specimen No. US-60-1

Sex: ♂; *length:* 4.21 m; *locality:* 57°46' N, 152°13' W (near Kodiak Island, Alaska); *date:* 20 May 1960; *collector:* Karl Niggol.

Stomach contents:

Pacific halibut *(Hippoglossus stenolepis)*

One, partially digested, weighing 10.5 kg.

Specimen No. US-61-1.

Sex: ♂; *length:* 7.60 m; *locality:* 37°29' N, 122°58' W (near Farallon Islands, California); *date:* 9 March 1961; *collector:* Clifford Fiscus.

Stomach contents:

California sea lion *(Zalophus californianus)*

One, represented by claws, vibrissae, and teeth. The growth layers and size of the canine teeth indicated that the animal was a 9-year-old male.

Elephant seal *(Mirounga angustirostris)*

Four, represented by claws, vibrissae, and hair.

Dall porpoise *(Phocoenoides dalli)*

One, represented by piece of dorsal fin and fragments of blubber. This was reported by Fiscus and Niggol (1965) as «fragments of one or more cetaceans, possibly Dall porpoise»; I have examined this material and confirmed its identity as *Phocoenoides.*

Specimen No. 605

Sex: ♂; *length:* 6.86 m; *locality:* 37°44' N, 122°46' W (off San Francisco); *date:* 15 May 1962; *collector:* Del Monte Fishing Co. (examined by Thomas McIntyre).

Stomach contents:

Steller sea lion *(Eumetopias jubatus)*

Three, represented by broken skulls and nearly complete skins. One of the skulls (Museum of Vertebrate Zoology No. 129694) is that of a 1-year-old animal, as determined by growth layers in the canine teeth; weight would be about 90 kg.

Specimen No. 832.

Sex: ♂; *length:* 7.24 m; *locality:* 37°57' N, 123°04' W (off San Francisco); *date* 1 July 1963; *collector: Del* Monte Fishing Co. (examined by Frank Maurer).

Stomach contents:

California sea lion *(Zalophus californianus)*

One, represented by teeth, vibrissae, and claws. Probably a young male.

Steller sea lion *(Eumetopias jubatus)*

One, represented by claws and vibrissae. Probably about 2 years old.

Elephant seal *(Mirounga angustirostris)*

One, represented by vibrissae.

Harbour porpoise *(Phocoena phocoena)*

Two, one adult represented by a section of the caudal peduncle and a flipper, and one less than half grown represented by a section of the anterior thoracic vertebrae with some ribs attached and a scapula with the head of the humerus attached.

Squid (Order Decapoda)

One, represented by fragments of body. Mantle length probably about 0.5 m.

Specimen No. 986.

Sex: ♀; *length:* 5.65 m; *locality:* 33°50' N, 120°31' W (off San Miguel Island, California); *date:* 9 January 1964; *collector:* Dale Rice.

Stomach contents:

Opah, or moonfish *(Lampris regius)*

Two, represented by skulls.

Carcharinid shark (Family Carcharinidae)

Two, represented by six pectoral and pelvic fins. Probably either blue sharks *(Prionace glauca)* or whitetip sharks *(Carcharhinus longimanus)*. The former species is the most commonly seen epipelagic shark in the area where this whale was collected.

Specimen No. 1965-4.

Sex: ♂; *length:* 7.40 m; *locality:* 34°23' N, 121°16' W (off Point Conception, California); *date:* 22 March 1965; *collector:* Kenneth Balcomb.

Stomach contents:

Minke whale *(Balaenoptera acutorostrata)*

One, represented by baleen and blubber.

Specimen No. 1966-145.

Sex: ♂; *length:* 7.31 m; *locality:* 37°00' N, 122°45' W (off San Francisco); *date:* 22 September 1966: *collector:* Del Monte Fishing Co. (examined by James Ekberg).

Stomach contents: None.

Specimen No. 3204.

Sex: ♂; *length:* 6.30 m; *locality:* 35°19' N, 120°55' W (off Morro Bay, California); *date:* 12 February 1966; *collector:* Richard Stroud.

Stomach contents: None.

Specimen No. 1967-157.

Sex: ♂; *length:* 6.57 m; *locality:* off San Francisco; *date:* 5 July 1967; *collector:* Del Monte Fishing Co. (examined by Bernard Lenheim).

Stomach contents:

California sea lion *(Zalophus californianus)*

One, represented by claws and one postcanine tooth.

Elephant seal *(Mirounga angustirostris)*

One, represented by one claw and hair.

Specimen No. 1967-175.

Sex: ♂; *length:* 6.07 m; *locality:* off San Francisco; *date:* 10 August 1967; *collector:* Del Monte Fishing Co. (examined by Bernard Lenheim).

Stomach contents:

Elephant seal *(Mirounga angustirostris)*

One, represented by claws and vibrissae.

Dall porpoise *(Phocoenoides dalli)*

One, represented by dorsal fin, flukes, and fragments of blubber and flesh.

Feeding Behavior

We have twice observed killer whales attacking California sea lions *(Zalophus californianus)*. The following observations are quoted from field notes:

On 25 May 1965, Kenneth C. Balcomb, aboard the chartered whale catcher boat *Sioux City,* made the following observations at 37°32' N, 123°03' W, southwest of the Farallon Islands, California:

«At 1305 we saw one big bull killer whale with a lopped over dorsal fin escorting two cows and a calf. Several hundred yards away a group of about 5 killer whales with calves were harassing a large male California sea lion.

«The adult killers were swimming around and around over and under this sea lion. When we first approached them, the sea lion leaped about seven feet out of the water a few feet from our bow and snapped violently towards [Captain] Don [Gamble] on the gun deck. As the killers kept going over and under him, occasionally ramming him slightly and sometimes pushing him down below the surface, the sea lion became more and more exhausted. We passed several times within a few feet of the animal and he made no attempt to get out of our way or dive. At 1350 one killer went right over him, another went immediately under him, and a third grabbed him and took him down. We saw no blood or anything — — whatever happened, happened far below the surface. We could not get a shot at the killers so we went on our way at 1405.»

On 9 February 1967, I made the following observations while the *Sioux City* lay at anchor at the Islas San Benito (28°19' N, 115°34' W), Baja California:

«From 1045 to 1100 a group of killer whales numbering at least six, including at least two calves and one adult male, appeared around the *Sioux City.* One had a small California sea lion in its jaws, and was followed by a swarm of over 100 western gulls *[Larus occidentalis]* which swooped down to pick up bits of coagulated blood each time the animal surfaced.»

Feeding behavior may also be inferred from the condition of the stomach contents. The fragmented condition of the cetacean remains in the whale stomachs indicates that the whales dismember these animals before ingesting them. Hancock (1965) described an incident in which killer whales attacked a minke whale in Barkley Sound, Vancouver Island, and stripped only the skin, dorsal fin, and tongue from the animal.

The presence of nearly entire skins of three yearling Steller sea lions in the stomach of one whale (specimen no. 605) indicates that these small seals were swallowed whole. The other seal remains that we found were too fragmentary to determine if the whales had swallowed the seals whole or dismembered them. Eschricht (1866) found that a killer whale from Denmark had swallowed whole harbor seals *(Phoca vitulina)*.

Conclusions

Six of the eight whales whose stomachs contained food were adult males. All six had only the remains of mammals in their stomachs, except for one which had the remains of one squid in addition to mammal remains. The stomachs of the one adult female and the one immature male (No. US-60-1) contained only fish and shark remains. I conclude that in the offshore coastal waters of the eastern North Pacific, adult male killer whales feed preponderantly on mammals.

Nishiwaki and Handa (1958) found that killer whales from the coastal waters of Japan fed mostly on fishes and cephalopods, but also fed on large numbers of cetaceans and pinnipeds. The larger whales took relatively more mammals. Zenkovich (1938) found remains of only bearded seal *(Erignathus barbatus)* and walrus *(Odobenus rosmarus)* in the stomachs of one adult male and one adult female killer whale in the Bering Sea.

In the eastern North Pacific killer whales are commonly encountered in only a few areas, most of which have high concentrations of marine mammals. They are regularly seen close to the Islas San Benito, Baja California, site of the largest known rookery of California sea lions, and second largest rookery of northern elephant seals. I have also observed them several times near San Miguel Island, California, site of another large rookery of California sea lions and elephant seals. Killer whales are seen frequently in the Aleutian Islands (K. Kenyon and C. Fiscus, pers. comm.), where there are many large rookeries of Steller sea lions.

In Puget Sound, where the killer whale population is probably denser than anywhere else in the world, the marine mammal population (mostly *Phocoena phocoena, Balaenoptera acutorostrata* and *Phoca vitulina,* and a few *Eumetopias jubatus)* does not appear large enough to provide a major proportion of the killer whale's diet. It is widely believed that runs of spawning salmon *(Oncorhynchus spp.)* are a major food there during the summer, but no data are available to support this assumption. «Namu», the adult male killer whale from Queen Charlotte Sound, British Columbia, which was kept at the Seattle Aquarium for a year, although offered several species of fishes, accepted only salmon during the first few months in captivity (E. Griffin, pers. comm.).

Although the northern fur seals on the Pribilof Islands constitute the world's largest aggregation of pinnipeds, biologists of the Bureau of Commercial Fisheries, working there regularly every summer, have seen few killer whales in the vicinity of the islands during the past 2 decades, and have never seen them close to the fur seal rookeries or hauling grounds, or attacking fur seals.

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Table 1. Number of each prey species represented in stomach contents of 10 killer whales (2 stomachs were empty)

	Specimen number								
Food species	US-60-1	US-61-1	605	832	986	1965-4	1967-157	1967-175	Total
California sea lion *(Zalophus californianus)*		1		1			1		3
Steller sea lion *(Eumetopias jubatus)*			3	1					4
Elephant seal *(Mirounga angustirostris)*		4		1			1	1	7
Harbor porpoise *(Phocoena phocoena)*				2					2
Dall porpoise *(Phocoenoides dalli)*		1						1	2
Minke whale *(Balaenoptera acutorostrata)*						1			1
Opah *(Lampris regius)*					2				2
Pacific halibut *(Hippoglossus stenolepis)*	1								1
Carcharinid shark *(? Prionace glauca)*					2				2
Squid *(Order Decapoda)*				1					1

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Right Whales in the Southeastern North Pacific

By

Dale W. Rice and Clifford H. Fiscus
U.S. Fish and Wildlife Service
Bureau of Commercial Fisheries
Marine Mammal Biological Laboratory
Sand Point Naval Air Station, Bldg. 192
Seattle, Washington 98115

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U.S. Fish and Wildlife Service
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Marine Mammal Biological Laboratory
Sand Point Naval Air Station, Bldg. 192
Seattle, Washington 98115

ABSTRACT

Right whales, *Balaena glacialis,* since being afforded complete protection by the International Whaling Commission in 1937, have been recorded only 10 times in the eastern North Pacific south of 50° N. lat. Five of these records are newly reported, including the southernmost known occurrence off Punta Abreojos, Baja California, Mexico.

INTRODUCTION

Right whales *Balaena glacialis* were formerly abundant in the North Pacific Ocean. From April through September, they were distributed mostly north of 50° N. lat., according to the logbook records of 19th Century American whalers (Townsend, 1935), who exploited them so relentlessly that they were nearly extinct by the turn of the century.

South of Vancouver Island, right whales were seldom reported. Scammon (1874) wrote «In former years the right whales were found on the coast of Oregon, and occasionally in large numbers; but their chief resort was upon what is termed the "Kodiak Ground", the limits of which extended from Vancouver's Island northwestward to the Aleutian Chain .... The few frequenting the coast of California are supposed to have been merely stragglers from their northern haunts. Some, indeed, have been taken (from February to April) as far south as the Bay of Sebastian Viscaino, and about Cedros or Cerros Island, both places being near the parallel of 29° north latitude.» Gilmore (1956) postulated that the main wintering ground of right whales in the eastern North Pacific was off the coast of Oregon and possibly northern California, where inclement winter weather discouraged whaling.

The Makah Indians, renowned aboriginal whalers living on the western shores of the Olympic Peninsula, Washington, knew the right whale (Swan, 1870; Waterman, 1920), but their common quarry was the gray whale *Eschrichtius gibbosus.*

Shore-based whalers on the coast of California in the 19th century took only an occasional right whale, some as far south as San Diego (D. S. Jordan, *In* Clark, 1887; Starks, 1922; Townsend, 1887).

Since the beginning of modern-style whaling off California in 1918, no right whales have been reported in the catches (Kellogg, 1931; Radcliffe, 1933). (Gilmore, 1956, said that a right whale was killed near the Farallon Islands in April 1924, but cited no authority.) Neither were any taken off Washington State from 1911 to 1925, when one shore station was in operation (Scheffer and Slipp, 1948).

Since 1937, when the right whale was accorded complete protection by the International Convention for the Regulation of Whaling, there have been only five published sightings of these animals: Gilmore (1956) observed one off La Jolla, California, on 31 March 1955. Niggol *(In* Fiscus and Niggol, 1965) reported four sightings totaling 22

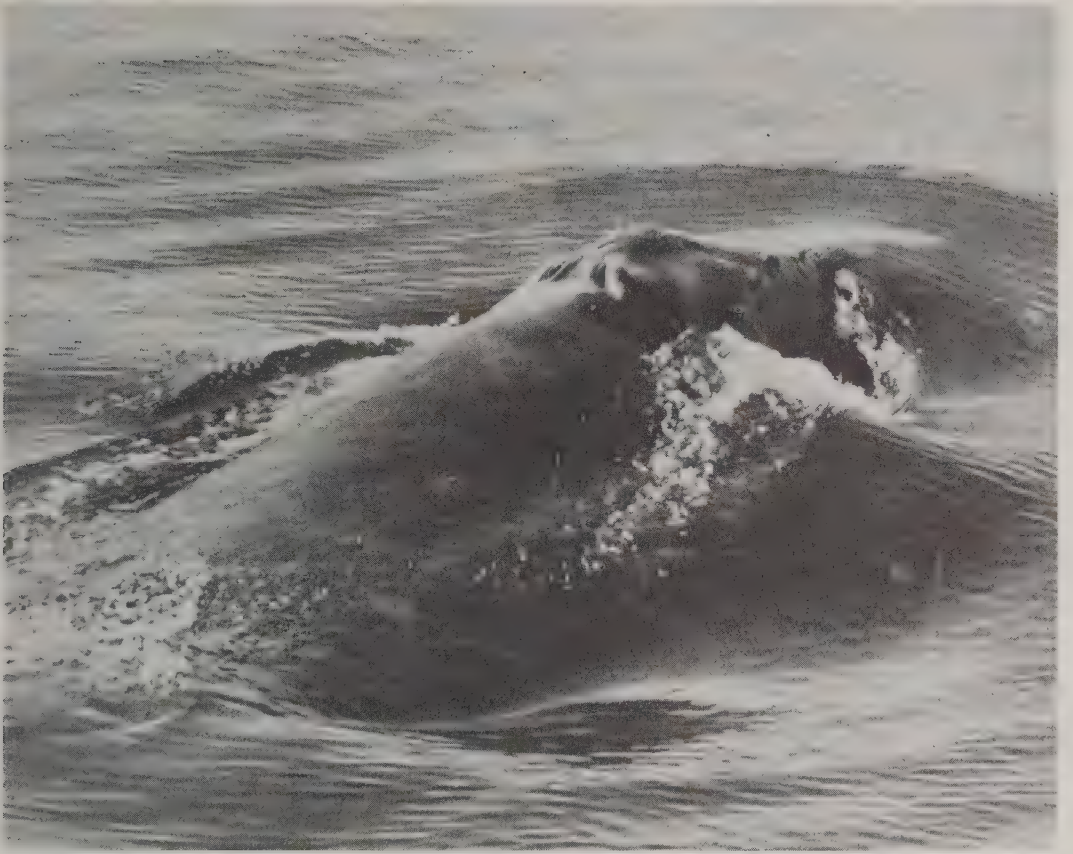

Figure 1. — Right whale, *Balaena glacialis* — one of two observed 12 km SW of Punta Abreojos, Baja California, Mexico, on 11 March 1965. Note the narrow arched rostrum bearing callosities (the «bonnet»), the arched lower lips with scalloped margins, and the widely separated blowholes. Photograph from a 35 mm Kodachrome transparency by Dale W. Rice.

individuals off the coasts of Oregon and Washington between 8 and 19 April 1959.

NEW RECORDS

We have observed right whales only twice during many months of whale-marking cruises and pelagic fur seal investigations since 1958, off the coasts of Washington, Oregon, California, and Baja California, mostly in winter and spring. Whalers operating out of Richmond, California, from April through October or November each year since 1956 have encountered right whales only three times. These five previously unpublished sightings are documented below:

1.) *13—15 May 1959, 37°25' N, 122°48' W, 16 miles (30 km) SW of Point Montara, California; water depth 55—60 fathoms (100—110 m).* Captain Grant Yost of the catcher boat *Allen Cody* saw one right whale, and several other whalers saw what was presumably the same animal. Its estimated length was slightly over 40 feet (ca. 13 m).

2.) *11 April 1963; 37°08' N, 123°05' W; 33 miles (61 km) W of Pigeon Point, California; water depth 400—500 fathoms (730—910 m).* Captain Edward Holloway of the *Allen Cody* encountered a small right whale, estimated length less than 30 feet (9 m).

3.) *10 May 1963; 37°20' N, 123°10' W, 24 miles (44 km) SSW of the Farallon Islands, California; water depth ca. 600 fathoms (1,100 m).* Captain Grant Yost of the *Dennis Gayle* and Edward Halloway of the *Allen Cody* saw one large right whale, estimated length ca. 45 feet (14 m).

4.) *11 March 1965; 26°39' N, 113°40' W, 6—7 miles (12 km) SW of Punta Abreojos, Baja California; water depth slightly less than 30 fathoms (54 m).* (See figure 1.) This sighting is the southernmost recorded occurrence of right whales in the southeastern North Pacific. Rice saw these two right whales while on a whale-marking cruise aboard the catcher boat *Lynnann.* The sea was almost dead calm (the wind was scarcely 1 knot from the SW), and skies were clear. The whales were sighted at 0830. The following details are quoted from field notes:

«About 6 or 7 miles southwest of Punta Abreojos we encountered two right whales, and spent 50 minutes chasing them and taking pictures (we did not attempt to mark them). They moved very leisurely, blowing 3—5 times, and then sounding for 4 or 5 minutes. A few times they raised their flukes when sounding, but usually they did not do so. At first they were rather suspicious and would not allow a really close approach, but later we approached within a few meters of them. Once one of them rolled on its side and exposed its head, including eye and lip, above water, possibly to look at us. Some *Lagenorhynchus [obliquidens]* were following them quite closely at times, and some red phalaropes *[Phalaropus fulicarius]* were close by. When first observed, the right whales were heading NW, but when pursued they frequently changed course. Their length was estimated at roughly 50 feet [15 m], or the size of a very large humpback, but they were 1/3 broader 'in the beam'. One was slightly smaller than the other — possibly they were a pair.»

5.) 17 January 1967; 48°20' N, 125°06' W, 15 miles (28 km) WSW of Cape Flattery, Washington; water depth 60 fathoms (110 m). Fiscus, while engaged in pelagic fur seal research aboard the M/V *Pribilof,* observed three right whales swimming south. Two were large, the other smaller.

CONCLUSIONS

After more than 30 years of legal protection, right whales remain on the brink of extinction in the eastern North Pacific. Populations in the western North Pacific may be slightly higher (Omura, 1958; Klumov, 1962).

ACKNOWLEDGMENTS

Captains Grant Yost and Edward Holloway, who formerly whaled for the Del Monte Fishing Company of Richmond, California, kindly provided details of their sightings of right whales.

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Eastern Atlantic Triglidae (Pisces, Scorpaeniformes)[1]

by

WILLIAM J. RICHARDS

U.S. BUREAU OF COMMERCIAL FISHERIES, TROPICAL ATLANTIC BIOLOGICAL LABORATORY,
MIAMI, FLORIDA 33149, U.S.A.

INTRODUCTION

The fishes considered in this study are of the family Triglidae and are commonly called gurnards or searobins. I exclude the armored searobins (family Peristediidae), which have been included in the Triglidae in many recent works (as GREENWOOD *et al.*, 1966). The material I examined was collected by the "Atlantide" Expedition (1945–46) along the West African coast from the Canary Islands to Angola (BRUUN, 1950); by the "Galathea" Expedition (1950) off West Africa, at depths less than 400 m (BRUUN, 1959; WOLFF, 1964); by the Guinean Trawling Survey (GTS) (WILLIAMS, 1964); by the R/V "Geronimo" (U.S. Bureau of Commercial Fisheries); and by the R/V "Pillsbury" (Institute of Marine Sciences, University of Miami) (BAYER, 1966). In addition, material was examined from the following museums[2]:

ANSP: The Academy of Natural Sciences of Philadelphia.
BMNH: The British Museum (Natural History), London.
ZMUC: Zoological Museum, the University, Copenhagen.
IRSNB: Institut Royal des Sciences Naturelles de Belgique.
SU: Stanford University, Division of Systematic Biology.
TABL: U.S. Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami.
UMML: Institute of Marine Sciences, University of Miami.
USNM: U.S. National Museum, Washington.

The material examined consisted of 552 specimens belonging to six species, all found off tropical West Africa. Two of these species are found in European marine waters, and all are allied with European gurnards. Five additional European species (126 specimens) were included in this study, so that all eastern Atlantic species could be treated. At least 37 names have been applied in past literature, either as genera or subgenera, to the fishes of this family. I have placed the eastern Atlantic species in three apparently well-defined genera and included subgeneric names for these species. My use of generic and subgeneric names is for the sake of convenience—such designations may require revision when a definitive worldwide study of gurnards is completed.

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[1] Contribution No. 55, U.S. Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Florida 33149.

[2] Uncataloged material is being retained at TABL for anatomical studies.

These species are:

Genus *Trigla* Linnaeus, 1758.
    lyra Linnaeus, 1758.
Genus *Chelidonichthys* Kaup, 1873.
  Subgenus *Chelidonichthys* Kaup, 1873.
    lucernus (Linnaeus, 1758).
    capensis (Cuvier *in* CUVIER & VALENCIENNES, 1829).
    gabonensis (Poll & Roux, 1955).
  Subgenus *Trigloporus* Smith, 1934.
    lastoviza (Bonnaterre, 1788).
  Subgenus *Eutrigla* Fraser-Brunner, 1938.
    gurnardus (Linnaeus, 1758).
  Subgenus *Aspitrigla* Fowler, 1925.
    cuculus (Linnaeus, 1758).
    obscurus (Bloch and Schneider, 1801).
Genus *Lepidotrigla* Günther, 1860.
    cavillone (Lacépède, 1802).
    cadmani Regan, 1915.
    carolae new species.

The gurnards found in European waters have been discussed extensively in several recent works. SVETOVIDOV (1936) reviewed the species and presented lengthy synonymies, with particular attention to their presence or absence in the Black Sea. FRASER-BRUNNER (1938) dealt with gurnards found near the British Isles and gave a subgeneric analysis. POLL (1947) described the species from Belgian waters; SOLJAN (1948) presented keys to Adriatic Sea species; LOZANO Y REY (1952) and ALBUQUERQUE (1954–56) discussed gurnards present in coastal waters off Spain and Portugal; BEN-TUVIA (1953) listed the species found in Israeli waters.

Studies of gurnards from West African waters have been limited because only recently have collecting efforts provided necessary specimens. FOWLER (1936) presented a comprehensive review of species from West Africa, but his studies were based primarily on literature and on European species and specimens. NORMAN & IRVINE (1947) gave keys, descriptions, and figures of the species inhabiting the waters adjacent to Gold Coast (present-day Ghana); CADENAT (1950) published brief descriptions of gurnards found along the coast of Senegal; ROUX (1957) and ROUX & COLLIGNON (1957) gave descriptions, keys, and figures of a few species; a report by POLL (1959) figured, described, and gave ecological notes on the fishes collected along the coast of the Congo; BLACHE (1962) listed species from the Gulf of Guinea between latitudes 4°N and 15°S.

The region between Gibraltar and Cape Verde appears to act as a northern barrier to the Gulf of Guinea endemics and as a southern barrier to some of the European species as well. Study in this area has been scanty, however, and only brief lists exist of species from localized areas (CHABANAUD & MONOD, 1927; MURRAY & HJORT, 1912). Three gurnards are known from the waters around the islands off Gibraltar and Cape Verde—the Madeiras, the Canaries, and the Cape Verde Islands (MAUL, 1949).

I followed counting and measuring methods defined by HUBBS & LAGLER (1958: 19–26) except for the following:

Standard length (abbreviated SL) was measured from the anterior tip of the snout or preorbital spines to the base of the caudal fin. Head length was measured from the anteriormost point on the snout to the most distant point of the opercular membrane or opercular spine. In many of the species, the suprascapular or nuchal spine extended even farther posteriad, but this extension was not used for this measurement. Interorbital width was measured as the least bony width. Suborbital width was measured from the orbit at the middle of the eye downward (perpendicularly) to the lower edge of the infraorbital bone. Cleithral spine length was measured from the anterior edge of the cleithrum posteriorly to the tip of the spine. Gillraker counts do not include rudimentary rakers. Diagonal scale rows were counted downward and backward from the second dorsal fin origin to the base of the anal fin and are expressed as the number above or below the lateral line.

I am indebted to the following for supplying material: JAMES E. BÖHLKE, WARREN C. FREIHOFER, J. P. GOSSE, JØRGEN G. NIELSEN, C. RICHARD ROBINS, ALWYNNE C. WHEELER, and FRANK C. WILLIAMS. GRADY REINERT made the illustrations. The manuscript was read and criticized by FREDERICK H. BERRY, JAMES E. BÖHLKE, BRUCE B. COLLETTE, and C. RICHARD ROBINS.

NOMENCLATURE

Much of the existing nomenclature of the seven species of European gurnards is inconsistent, mainly because early investigators used a few basic names and applied them indiscriminately to various species. Also, many of the morphological characters used in early studies did not separate the species into the taxa we recognize today. It has been possible to clarify in the present study some of these problems and provide nomenclatural stability.

The criteria of priority and stability have been followed without regard to the first reviser concept, which would tend to interfere with priority and stability. As a result, all but one of the Linnaean names of the family Triglidae are used as senior synonyms.

Five European species of gurnards were described by LINNAEUS (1758): *Trigla lyra*, *T. gurnardus*, *T. cuculus*, *T. lucerna*, and *T. hirundo*. LINNAEUS' descriptions of *T. lyra* and *T. gurnardus* are sufficient to identify these two species, and the holotype of *gurnardus* is extant (WHEELER, 1958: 239 and personal communication). The descriptions of the remaining three species placed in *Trigla* by LINNAEUS (*cuculus*, *lucerna*, and *hirundo*) are very brief, and insufficient to separate the species. The holotype of *lucerna* is extant in the British Museum (WHEELER, 1958: 239 and personal communication); on this basis I restrict and define *lucerna*. Types for *hirundo* apparently do not exist, but in the original description LINNAEUS (1758) referred to ARTEDI (1738) who cited WILLUGHBY & RAY (1686); this latter work presented a reasonable description and figure of this species identifiable as conspecific with *lucerna*. Because *T. lucerna* was described before *T. hirundo* by LINNAEUS, and inasmuch as the holotype of *lucerna* is extant, I refer *hirundo* to junior synonomy of *lucerna*. Further, FRASER-BRUNNER (1938) may be considered the first reviser—he said that *T. hirundo* Linnaeus was a junior synonym of *T. lucerna* Linnaeus.

T. cuculus Linnaeus presented a much more difficult problem. BRÜNNICH (1768) used four of the Linnaean names for gurnards, and his descriptions included sufficient diagnostic characters to identify his species. His description of *hirundo* is actually that of a young *gurnardus*, his *cuculus* is *lucerna*, his *lucerna* is *Chelidonichthys obscurus* (Bloch and Schneider), and his *gurnardus* is *C. gurnardus* (Linnaeus). In his species descriptions, BRÜNNICH did not cite any authors, with the result that many subsequent workers have attributed these names to him. I interpret the four names as Linnaean names since BRÜNNICH cited LINNAEUS (1766) in his introduction and used identical names. I conclude, therefore, that BRÜNNICH misidentified his *hirundo*, his *cuculus*, and his *lucerna*, but correctly identified his *gurnardus*.

BLOCH (1783) described as *T. cuculus* a specimen that was undoubtedly a young *gurnardus*. BONNATERRE's (1788) description of *T. cuculus* Linnaeus was also that of a young *gurnardus*. GMELIN's (1789) description of *T. cuculus* was similar to the description given by LINNAEUS. BLOCH (1793) described and figured *T. cuculus* Linnaeus, but named it *T. pini*, a name that has been subsequently applied to this species about as often as *T. cuculus* Linnaeus. CUVIER, *in* CUVIER & VALENCIENNES (1829), discussed this problem of *cuculus* and arrived at the opinion (with which I concur) that ARTEDI and LINNAEUS confused *cuculus* of BELLONIUS (= *T. cuculus* Linnaeus?) with *cuculus* of RONDELET (= *T. obscura* Bloch & Schneider) and on this foundation erected *T. cuculus* Linnaeus. I apply the Linnaean name *T. cuculus* to this species by designating a neotype below in accordance with Article 75 of the International Code of Zoological Nomenclature.

Many workers have referred to *C. lastoviza* (Bonnaterre, 1788) as *T. lastoviza* Brünnich, 1768, but this name was proposed not as a scientific name, but as a common name, by BRÜNNICH. LACÉPÈDE (1802) used *lastoviza* for this species in combination with *Trigla* but made no reference to any other author. *Mullus imberbis* Rondelet, which is described and figured by WILLUGHBY & RAY (1686) is *C. lastoviza* also. *Mullus imberbis* Linnaeus, 1758, is an *Apogon*, however, based on the description by ARTEDI (1738), which in turn refers to *Mullus imberbis, sive Rex Mullorum* in Willughby & Ray (1686).

Of the remaining two European gurnards, one was first described as *T. lucerna* by BRÜNNICH and referred to as *T. lucerna* Brünnich by BONNATERRE. Because this name is unavailable by homonymy, the first available name for this species is *T. obscura* Bloch & Schneider, 1801. The other species was first described by LACÉPÈDE (1802) as *T. cavillone*, which I place in the genus *Lepidotrigla* Günther.

A nomenclatural problem involving the two species of West African *Lepidotrigla* has been resolved in this study. REGAN (1915) described *L. cadmani* from off Lagos, Nigeria. BLACHE & DUCROZ (1960) recognized two species from the Gulf of Guinea —*L. cadmani* Regan, and one new species, *L. laevispinnis*. The two species are easily separable—one has a scaleless breast and serrated first dorsal spine, the other has a scaly breast and smooth first dorsal spine. BLACHE & DUCROZ referred to the former as *L. cadmani* Regan and to the latter as *L. laevispinnis*. Examination of the syntypes of *L. cadmani*, the description by REGAN (1915), and a comparison with the description by BLACHE & DUCROZ (1960) leave no doubt that *L. laevispinnis* is a junior synonym of *L. cadmani*. I have, therefore, described the form with naked breast and serrated first dorsal spine as a new species, *L. carolae*, below.

In the species accounts below, I attempted to include all the names applied to these gurnards; in most accounts, I did not include the same name when used by different authors. I was unable to allocate the name *Trigla fagianus* Rafinesque, 1810 to any species. Thus I consider it as a *nomen dubium*.

Key to the adult Triglidae, eastern Atlantic Ocean

A. Spiny bucklers present along bases of spinous and soft dorsal fin...Subfamily Triglinae

1a. Swimbladder thin walled with muscle bands extending laterally on each side, cleithral spine very long and strong (greater than 15% SL) (genus *Trigla* Linnaeus)..........................one species, *Trigla lyra* Linnaeus

1b. Swimbladder with thick strong walls and with muscle bands extending laterally along each side, cleithral spine short and weak (less than 12% SL).. 2

2a. Head with a deep occipital groove (fissure posterodorsal of eye); body scales large, usually less than 60 along lateral line (Genus *Lepidotrigla* Günther).. 9

2b. Head without deep occipital groove; body scales small, usually more than 60 along lateral line (Genus *Chelidonichthys* Kaup)........... 3

3a. Lateral-line canal with extensive branches extending transversely over the sides of the body (Subgenus *Trigloporus* Smith)....................................one species, *Chelidonichthys lastoviza* (Bonnaterre)

3b. Lateral-line canal normal, no extensive branches.................. 4

4a. Lateral-line scales with spinate median keels or transversely expanded 5

4b. Lateral-line scales normal without spinate median keels or transverse expansions (Subgenus *Chelidonichthys* Kaup)..................... 6

5a. Lateral-line scales with a spinate median keel (Subgenus *Eutrigla* Fraser-Brunner).............one species, *Chelidonichthys gurnardus* (Linnaeus)

5b. Lateral-line scales expanded into transverse plates without median spines (Subgenus *Aspitrigla* Fowler) 8

6a. Breast and belly fully scaled, approximately eight scale rows above lateral line, body scales not embedded and slightly deciduous . . . . *Chelidonichthys gabonensis* (Poll and Roux)

6b. Breast naked, belly partially scaled (about 60%), approximately 15 scale rows above lateral line, body scales embedded and firmly attached 7

7a. Total gill rakers on first gill arch (not including rudiments) 7 to 11 . . . . *Chelidonichthys lucernus* (Linnaeus)

7b. Total gill rakers on first gill arch (not including rudiments) 15 to 19 . . . . *Chelidonichthys capensis* (Cuvier)

8a. First dorsal fin with the second spine elongated as a long filament; first dorsal spine smooth anteriorly. Lateral-line scales moderately large and high, distance between top of lateral-line scale and dorsal fin base 100% of total height of lateral-line scale . . . . *Chelidonichthys obscurus* (Bloch and Schneider)

8b. First dorsal fin with the second spine not greatly elongate; first dorsal spine serrate anteriorly; lateral-line scales large and extremely high, distance between top of lateral-line scale and dorsal fin base 25% to 50% of total height of lateral-line scale . . . . *Chelidonichthys cuculus* (Linnaeus)

9a. Breast naked; first dorsal spine serrate anteriorly; dorsal and anal softrays each 14–16, modally 15; vertebrae 30–32, modally 31 10

9b. Breast scaled; first dorsal spine smooth anteriorly; dorsal and anal softrays each 13–15, modally 14; vertebrae 29–31, modally 30 . . . . *Lepidotrigla cadmani* Regan

10a. Cleithral spine long (13.2–16.0% SL); all body scales strongly attached and ctenoid . . . . *Lepidotrigla cavillone* (Lacépède)

10b. Cleithral spine short (9.1–12.7% SL); body scales, loosely attached, cycloid on belly and lower flanks, ctenoid above and immediately below lateral-line scales . . . . *Lepidotrigla carolae* n. sp.

SPECIES ACCOUNTS

Trigla lyra Linnaeus

(Fig. 1)

Trigla lyra Linnaeus, 1758: 300 (original description; Mari Britannica).

Material (Museum number, station number, locality, depth, and date followed by number of specimens and standard length range in parentheses):

ANSP: 11703, Mediterranean, Bonaparte Collection No. 98.—1(213).
SU: 20912, Naples, Italy.—2(191–203).

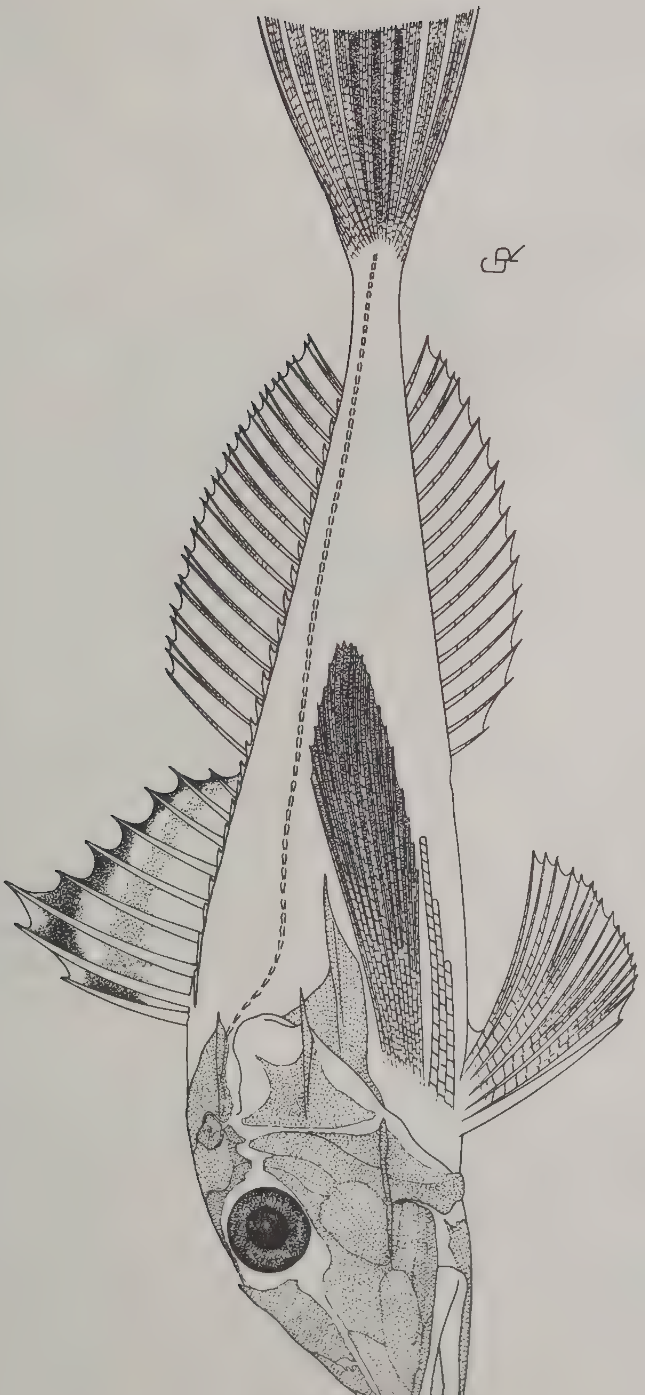

Fig. 1. *Trigla lyra* Linnaeus.
TABL 101054, Gulf of Guinea,
"Geronimo" Cruise 2, St. 247,
4°38′S, 11°02′E, 254 mm SL.

"Guinean Trawling Survey I":

USNM: 201765, Transect 1, St. 7, 12°06′N, 17°22′W, 200 m, 12.12.1963.— 1(181).
201766, Transect 16, St. 8, 5°17′N, 9°55′W, 380–400 m, 4.11.1963.— 6(163–183).
201767, Transect 17, St. 7, 4°38′N, 9°13′W, 200 m, 2.11.1963.— 16 (103–192).

"Guinean Trawling Survey II":

Transect 7, St. 2, 9°28′N, 14°22′W, 30 m, 15.5.1964.—1(192).
Transect 17, St. 7, 4°39′N, 9°15.5′W, 200 m, 21.4.1964.—2(130–132).
Transect 17, St. 8, 4°37.5′N, 9°15′W, 400 m, 22.6.1964.—2(160–163).
Transect 27, St. 8a, 4°41.5′N, 2°47′W, 400 m, 20.3.1964.—1(151).
Transect 28, St. 8, 4°21′N, 2°08′W, 400 m, 18.3.1964.—4(151–191).
Transect 29, St. 7a, 4°16′N, 1°29′W, 200 m, 12.3.1964.—1(153).
Transect 61, St. 8, 4°55′S, 11°20′E, 400 m, 26.4.1964.—4(171–208).

"Pillsbury":

UMML: 15602, St. 73, 4°38′N, 9°20′W, 4.6.1964.—2(156–182).
16881, St. 83, 4°59′N, 9°37′W, 5.6.1964.—2(109–113).
21438, St. 255, 3°49′N, 7°38′E, 14.5.1965.—13(158–200).

"Geronimo":

TABL: 101050, Cruise 2, St. 198, 1°28′S, 8°25′E, 300 m, 3.9.1963.—2(80–157).
101051, Cruise 2, St. 204, 1°56′S, 8°47′E, 300 m, 4.9.1963.—1(169).
101052, Cruise 2, St. 220, 3°02′S, 9°21′E, 300 m, 6.9.1963.—5(85–265).
101053, Cruise 2, St. 228, 3°31′S, 9°53′E, 400 m, 7.9.1963.—2(201–230).
101054, Cruise 2, St. 247, 4°38′S, 11°02′E, 400 m, 9.9.1963.—3(227–284).

Diagnosis: The only species of the monotypic genus *Trigla*, having a thin-walled swimbladder; a long and strong cleithral spine, 16.6–19.3% SL; lateral-line scales with spines; breast scaleless; belly partially scaled; pectoral fin long, reaching anal fin origin; 31–32 vertebrae, 11–12 precaudal, 19–21 caudal.

Distribution: One of the widest-ranging gurnards in the eastern Atlantic (Fig. 2), *T. lyra* is found north to the North Sea (NYBELIN, 1950; NIELSEN, 1963); around the British Isles (FRASER-BRUNNER, 1938); off the southern coast of Europe and throughout the northern Mediterranean (LOZANO Y REY, 1952; BEN TUVIA, 1953; ALBUQUERQUE, 1954–56); absent from the Black Sea (SVETOVIDOV, 1936). *T. lyra* ranges southward from Gibraltar (MURRAY & HJORT, 1912) and has been reported from Cape Blanc, Mauritania (CHABANAUD & MONOD, 1927) and at Madeira (MAUL, 1949). Common in the Gulf of Guinea, the species has been reported as far south as Walvis Bay, South West Africa, by SVETOVIDOV (1936), POLL (1959) collected specimens as far south as latitude 19°52′S (Angola), and SANCHES (1966) reports it as common off Angola.

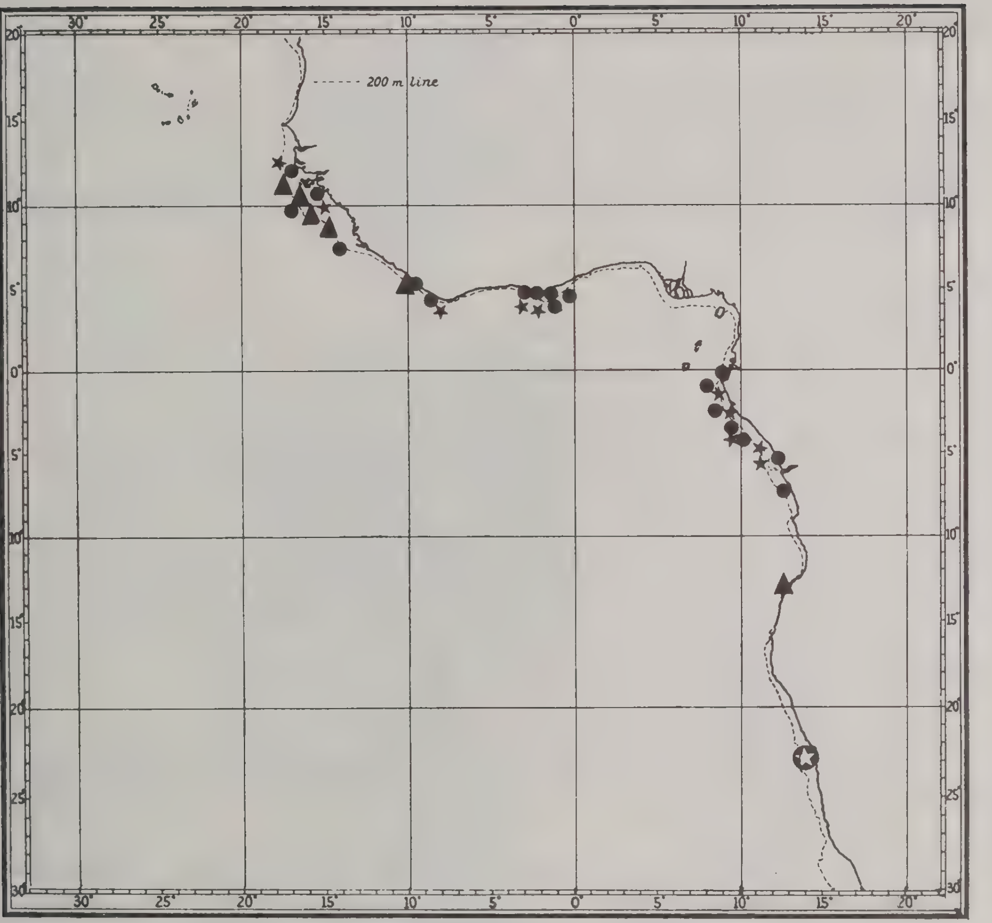

Fig. 2. Distribution of *Trigla* and *Chelidonichthys* in the tropical eastern Atlantic based on specimens examined. *T. lyra* (solid stars), *C. gabonensis* (circles), *C. lastoviza* (triangles), and *C. capensis* (open star).

Discussion: Comparisons between specimens from the Mediterranean and from the Gulf of Guinea revealed no differences greater than those between specimens from a single sample. This species is found in deep waters in the Gulf of Guinea: specimens were collected from 4 GTS stations at 200 m, 4 GTS stations at 400 m, 1 GTS station at 30 m, 3 "Geronimo" stations at 300 m, and 2 "Geronimo" stations at 400 m. Temperatures at the "Geronimo" stations ranged from 9.0 to 11.6°C, salinity from 34.90‰ to 35.12‰, and dissolved oxygen from 1.4 to 1.7 ml/L. Bottom types were unrecorded.

Chelidonichthys (*Trigloporus*) *lastoviza* (Bonnaterre)

(Fig. 3)

Trigla lastoviza Bonnaterre, 1788: 147 (original description; Mediterranean).
Trigla lineata Gmelin, 1789: 1345 (original description; Cornubiam).
Trigla adriatica Gmelin, 1789: 1345 (original description; Adriatic Sea).
Trigla lastoviza Lacépède, 1802: 340, 349 (original description; Atlantic Ocean and Mediterranean).

Material:
SU: 2369, Venice, Italy.—7(104–166).
24085, Baia Formosa, west of Funchal, Madeira.—2(113–130).
64921, Venice, Italy.—1(91).
ANSP: 95586, Baia Formosa, west of Funchal, Madeira.—1(154).
11718–31, Mediterranean, Bonaparte Collection No. 102.—13(79–175).
ZMUC: P79968–70, Morocco.—3(125–132).
P79971–73, Tunis, 1938.—3(124–132).
IRSNB: 7177, Angola, Bay of Elephants, 30 m, 4.11.1937.—2(143–154).
TABL: 101049, Cuma Beach near Pozzuoli, Naples, Italy, 15–20 m, 21–22.7.1966.—7(46–164).
UMML: 8475, Spain, Blanes Market, 26.8.1960.—1(162).

"Guinean Trawling Survey I":
USNM: 201768, Transect 3, St. 3, 10°55′N, 16°49′W, 40 m, 7.12.1963.—1(174).
201767, Transect 4, St. 3, 10°26′N, 16°21′W, 40 m, 5.12.1963.—2(160–166).
201770, Transect 4, St. 5, 10°17′N, 16°30′W, 70 m, 6.12.1963.—9(125–165).
201771, Transect 5, St. 3, 9°53′N, 15°56′W, 40 m, 1.12.1963.—1(194).
201772, Transect 5, St. 4, 9°47′N, 16°02′W, 50 m, 1.12.1963.—1(152).
201773, Transect 6, St. 3, 9°35′N, 15°18′W, 40 m, 29.11.1963.—5(153–168).
201774, Transect 7, St. 3, 9°13′N, 14°35′W, 40 m, 26.11.1963.—1(189).
201775, Transect 7, St. 5, 9°03′N, 14°49′W, 70 m, 27.11.1963.—3(116–144).
201776, Transect 8, St. 3B, 8°43′N, 14°03′W, 40 m, 24.11.1963.—3(163–173).
201777, Transect 8, St. 5, 8°32′N, 14°17′W, 70 m, 25.11.1963.—4(140–184).
201778, Transect 8, St. 6A, 8°28′N, 14°21′W, 100 m, 25.11.1963.—1(206).
201779, Transect 15, St. 6, 5°43′N, 10°22.5′W, 100 m, 6.11.1963.—1(219).

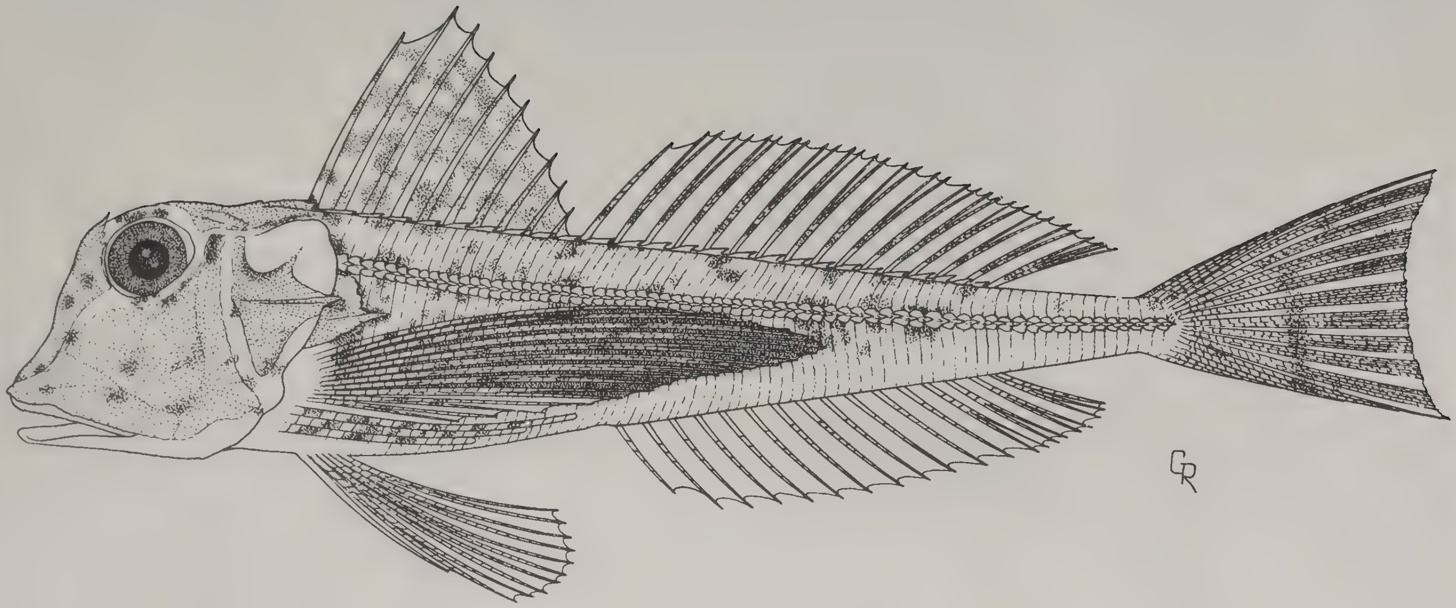

Fig. 3. *Chelidonichthys lastoviza* (Bonnaterre). USNM 201771, Gulf of Guinea, "Guinean Trawling Survey I", Trans. 5, St. 3, 9°53′N, 15°56′W, 194 mm SL.

Diagnosis: A species of *Chelidonichthys* having lateral-line scales with spines; lateral-line canal with extensive vertical branches forming transverse grooves along the body; pectoral fin long, 34.0–46.8% SL; breast variably naked to fully scaled; belly fully scaled; 33–35 vertebrae, 12–14 precaudal, 20–22 caudal.

Distribution: Probably the most widely dispersed gurnard of the eastern Atlantic (Fig. 2), ranges north to Norway (Barth, 1962) and south along the Low Countries (Poll, 1947), British Isles (Fraser-Brunner, 1938), Mediterranean (Svetovidov, 1936), off Gibraltar (Murray & Hjort, 1912), Azores (Fowler, 1936), Madeira (Maul, 1949), Cape Blanc (Chabanaud & Monod, 1927), the Gulf of Guinea (Blache, 1962; Crosnier & Berrit, 1966), and south to the Bay of Elephants, Angola (Poll, 1959).

Discussion: This species is closely related to *C. africanus* (Smith) from South Africa. I was unable to examine specimens of *C. africanus*, but Smith (1934) presented a table of comparisons between *C. africanus* and *C. lastoviza* made by the late J. R. Norman of the British Museum. I selected a few specimens from the geographic range of *C. lastoviza* and compared the characters with the data presented by Smith for *C. africanus*. Overlap was found in all but one character—humeral spine in head (I assumed that Smith's "pectoral times head" is equivalent to pectoral fin length divided by head length). Smith did not define his humeral spine-length measurement so this difference may not be valid.

C. lastoviza is not common in the southern Gulf of Guinea and has not been recorded south of Angola; therefore, the two species may be allopatric. Additional specimens are needed from these areas for comparison with *C. africanus* before valid taxonomic judgments can be made. Morphometric and meristic characters of *C. lastoviza* collected in the region of Banyuls, France, were reviewed by Monteiro (1957). I summarized meristic characters of my specimens in Tables 1, 2, and 3 (pp. 112–113).

Ecologically *lastoviza* appears to be confined to the continental shelf in the Gulf of Guinea. At the 12 GTS stations where this species was collected, depths were 40 m at 6 stations, 50 m at 1, 70 m at 3, and 100 m at 2.

Chelidonichthys (Eutrigla) gurnardus (Linnaeus)

(Fig. 4)

Trigla gurnardus Linnaeus, 1758: 301 (original description; Oceano Britannica).

Trigla grunniens Lapépède, 1802: 340, 358 (original description; Atlantic Ocean and Mediterranean).

Trigla milvus Lapédède, 1802: 340, 362 (original description; Atlantic Ocean and Mediterranean).

Trigla blochii Yarrell, 1836: 50 (original description; English Channel and Mediterranean).

Trigla milvus Risso, 1826: 395 (original description; Mediterranean).

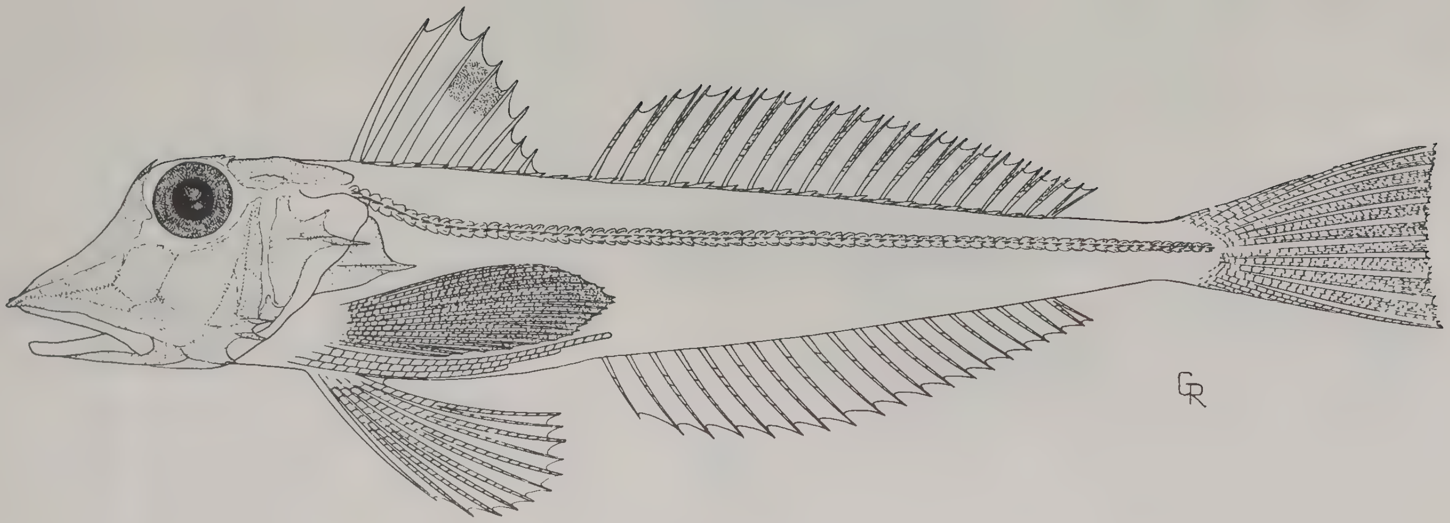

Fig. 4. *Chelidonichthys gurnardus* (Linnaeus). ZMUC P79974, Morocco, 116 mm SL.

Material:
SU: 1322, Venice, Italy.—4(103–112).
64922, Venice, Italy.—2(105).
ANSP: 11685–9, Mediterranean, Bonaparte Collection No. 97.—5(85–127).
ZMUC: P79974, Morocco.—1(116).

Diagnosis: A species of *Chelidonichthys* having lateral-line scales with spinate median keels; breast naked, belly partially scaled; short pectoral fins not reaching anal fin origin, 23.0–27.3% SL; 37–39 vertebrae, 11–13 precaudal, 25–27 caudal.

Types of Nominal Species: *Trigla gurnardus* Linnaeus. Holotype BMNH 1853. 11.12:15, 243 mm (Wheeler, 1958). I did not examine this specimen, but a photograph of it supplied to me by Alwynne C. Wheeler is presented (Pl. VII A). Other types not examined.

Distribution: This species is found from northern Norway, south into the western Baltic Sea, in the North Sea, on the western and southern coasts of Iceland, around the British Isles, on the Atlantic coast of Europe, in the Mediterranean, and in the Black Sea (Nybelin, 1950; Poll, 1947; Fraser-Brunner, 1938; Svetovidov, 1936; Andriiashev, 1954). *C. gurnardus* has not been recorded south of Gibraltar.

Discussion: *C. gurnardus* apparently undergoes extreme growth changes, which has led to some confusion on the part of early investigators. Svetovidov (1936) gave an account of these differences in ontogeny; I agree with his conclusions. Meristic characters of the specimens I examined are shown in Tables 1, 2, and 3 (pp. 112–113).

Chelidonichthys* (*Aspitrigla*) *cuculus (Linnaeus)

(Fig. 5)

Trigla cuculus Linnaeus, 1758: 301 (original description; Mediterranean).
Trigla pini Bloch, 1793: 130 (original description; Holland).
Trigla sicula Swainson, 1838: 426 (original description; Sicily).

Material:
SU: 2531, Europe.—1(165).
20937, Naples, Italy.—1(188).
ANSP: 11690–95, Mediterranean, Bonaparte Collection No. 85.—6(101–165).
ZMUC: P79975, Morocco.—1(139).
BMNH: 1963:5.14:696–7, 42°34′40″N, 3°09′30″E, 63–67 m, Banyuls-sur-Mer, France, 15.5.1961.—2(173–214).

Diagnosis: A species of *Chelidonichthys* with platelike, lateral-line scales expanded vertically—the distance between top of scale and dorsal fin base is about 25 to 50% of total height of scale; second dorsal spine not elongated; first dorsal spine serrate anteriorly; 36–37 vertebrae, 13–14 precaudal, 22–23 caudal.

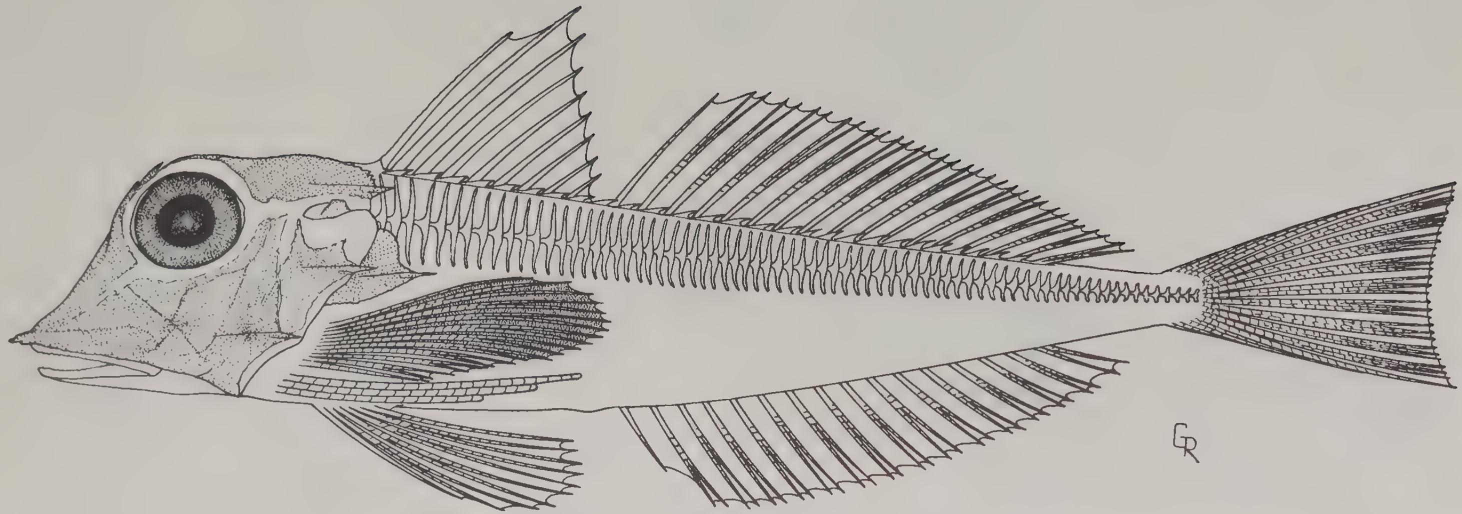

Fig. 5. *Chelidonichthys cuculus* (Linnaeus). Neotype BMNH 1963.5.14:696, Banyuls-sur-Mer, France, 173 mm SL.

Types of Nominal Species: *Trigla cuculus* Linnaeus. Neotype, herein designated: BMNH 1963.5.14:696 (♂, 173), Mediterranean Sea off Banyuls-sur-Mer, France 42°34′40″N to 42°41′10″N by 3°9′30″E, depth 63–67 m, gray-brown mud bottom, 15 May 1961. This specimen is illustrated (Fig. 5), a photo shown (Plate VII C), and is described as follows: 9 dorsal spines, 17 dorsal soft rays, 16 anal rays, 11 plus 3 free pectoral rays, 1 spine and 5 pelvic soft rays, 11 principal caudal rays, 27 spines (bucklers) along base of dorsal fins, 8 gill rakers on the lower arch, 72 lateral-line scales, about 15 scales above lateral line and about 40 scales below (counted diagonally), breast partially scaled, belly fully scaled, prepectoral area naked, and prevomerine teeth present. Body measurements in millimeters with percentage of standard length in parentheses are: head length 53.1 (30.7), length of orbit 19.3 (11.2), interorbital width 6.5 (3.8), body depth 32.2 (18.6), depth of caudal peduncle 7.9 (4.6), length of caudal peduncle 24.3 (14.0), predorsal length 59.3 (34.3), length of first dorsal base 30.1 (17.4), length of second dorsal base 60.6 (35.0), length of anal base 58.2 (33.6), length of longest dorsal spine 34.6 (20.0), length of longest pectoral ray 49.7 (28.7), depth of head 33.3 (19.2), head width 29.3 (16.9), snout length 23.2 (13.4), postorbital length of head 16.2 (9.4), suborbital width 12.4 (7.2), height of cheek 16.5 (9.5), length of eye 15.8 (9.1), length of upper jaw 22.3 (12.9), and length of cleithral spine 15.8 (9.1). Other types not examined.

Distribution: *C. cuculus* extends southward from the North Sea along the Atlantic coast of Europe, throughout the Mediterranean, and possibly in the Black Sea (SVETOVIDOV, 1936); southward to Cape Blanc, Mauritania (CHABANAUD & MONOD, 1927); has been recorded from Madeira (MAUL, 1949).

Discussion: Meristic characters are shown in Tables 1, 2, and 3 (pp. 112–113). Similar modified lateral-line scales found in both *C. cuculus* and *C. obscurus* seem to show a close relation between the two, some meristic characters, the general shape of the preorbital bone, and the shape of the body do not support this view.

Chelidonichthys* (*Aspitrigla*) *obscurus (Bloch & Schneider)

(Fig. 6)

Trigla obscura Bloch & Schneider, 1801: 16 (original description; Mediterranean).
Trigla cuculus Risso, 1826: 394 (original description after Rondelet; Mediterranean).
Trigla bracanthus Swainson, 1838: 421 (original description; Sicily).

Material:

ANSP: 11698–702, Mediterranean, Bonaparte Collection No. 96.—5(82–146).
11706–717, Mediterranean, Bonaparte Collection No. 100.—1(75).
ZMUC: P79976, Morocco.—1(205).
TABL: 101048, Cuma Beach near Pozzuoli, Naples, Italy, 15–20 m, 21–22.7. 1966.—10(88–139).

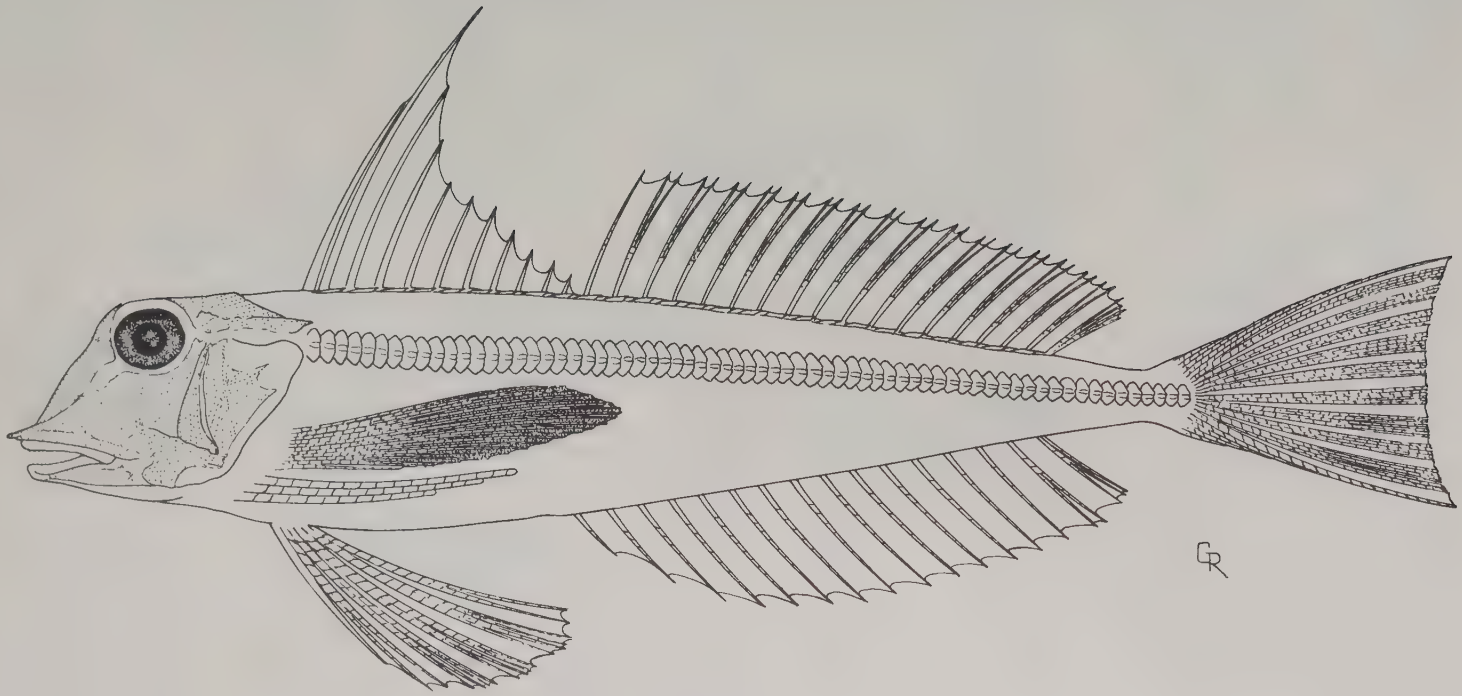

Fig. 6. *Chelidonichthys obscurus* (Bloch & Schneider). TABL 101048, Naples, Italy, 139 mm SL.

Diagnosis: A *Chelidonichthys* with expanded, platelike lateral-line scales—the distance between top of scale and dorsal fin base 100% (usually greater) of total height of scale; second dorsal spine elongated as a long filament; first dorsal spine smooth anteriorly; 36–37 vertebrae, 12–13 precaudal, 23–24 caudal.

Distribution: Extends northward to the British Isles (Fraser-Brunner, 1938) and is common in the Mediterranean and around the Iberian Peninsula (Lozano y Rey, 1952 and Albuquerque, 1954–56; Svetovidov, 1936). *C. obscurus* apparently ranges south to Cape Blanc, Mauritania, and the Madeiras (Fowler, 1936), although the species does not appear on lists by Chabanaud & Monod (1927) and Maul (1949).

Discussion: Meristic characters of the specimens I examined are shown in Tables 1, 2, and 3 (pp. 112–113). The extreme elongation of the anterior dorsal spines is unique to this species—this elongation becomes greater with age and apparently is not a sexual character.

Chelidonichthys* (*Chelidonichthys*) *lucernus (Linnaeus)

(Fig. 7)

Trigla lucerna Linnaeus, 1758: 301 (original description; Northern Ocean).
Trigla hirundo Linnaeus, 1758: 301 (original description; Atlantic Ocean).
Trigla corvus Rafinesque, 1810: 32 (original description; Sicily).
Trigla swainsonii Leach, 1813 (original description). (I did not see the publication—see Swainson, 1838, p. 419.)
Trigla laevis Montagu, 1816 (original description). I did not see the publication—see Swainson, 1838, p. 419.)
Trigla corvus Risso, 1826: 398 (original description after Rondelet; Mediterranean).
Trigla microlepidota Risso, 1826: 399 (original description; Mediterranean).
Trigla poeciloptera Cuvier *in* Cuvier & Valenciennes, 1829: 47 (original description; Dieppe).
Trigia hyrax Pallas, 1831: 233 (original description; Black Sea).
Trigla corax Bonaparte, 1834: 94 (original description; Mediterranean).
Trigla pauciradiata Bennett, 1835: 91 (original description; Black Sea, Trebizond).
Trigla laevis Bonaparte, 1845: 61 (original description; Mediterranean).

Material:
SU: 1977, Venice, Italy.—4(139–167).
20903, Naples, Italy.—2(182–190).
ANSP: 11684, Beirut, Syria.—1(121).
ZMUC: P79977–81, Tunis, V:1938,—5(140–258).
TABL: 101047, Cuma Beach near Pozzuoli, Naples, Italy, 15–20 m, 21–22.7.1966, —10(83–142).

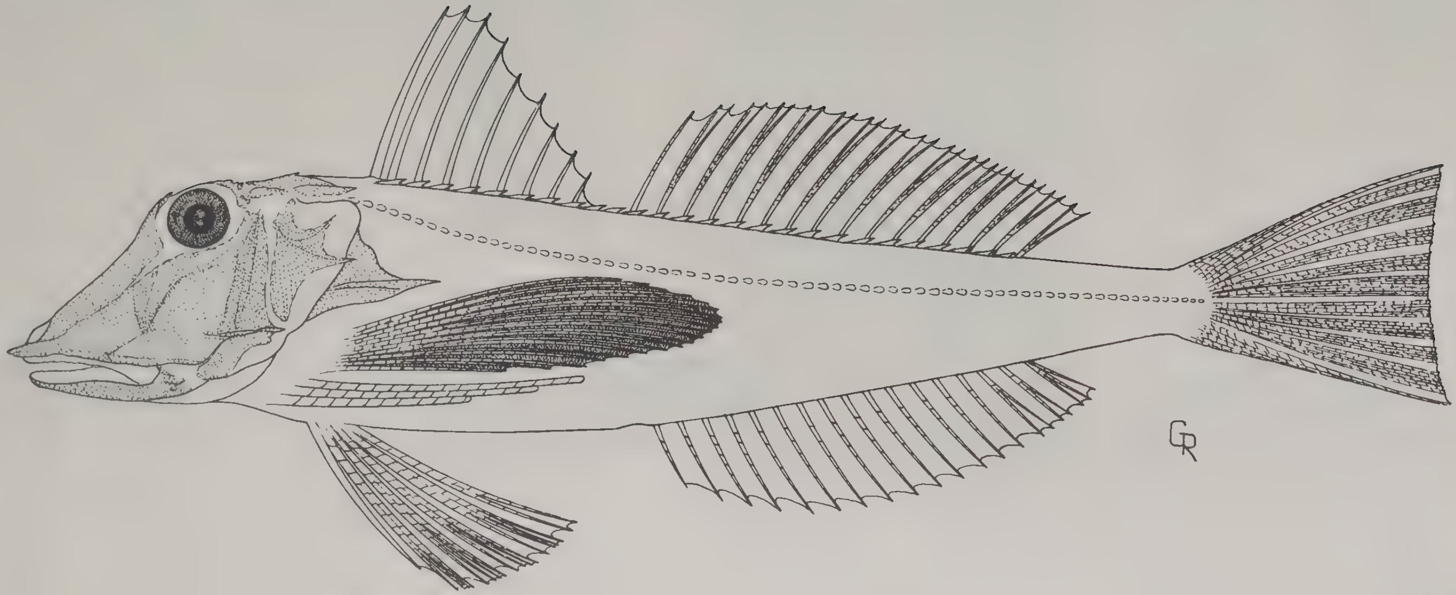

Fig. 7. *Chelidonichthys lucernus* (Linnaeus).
TABL 101047, Naples, Italy,
142 mm SL.

Diagnosis: A species of *Chelidonichthys* with normal lateral-line scales lacking spines or platelike expansions; swimbladder with no accessory branches; 7–11 gill rakers; long pectoral fins, 32.0–42.2% SL; breast naked and belly partially scaled; embedded body scales, 18–20 above lateral line and 37–60 below lateral line (diagonal count); 33–34 vertebrae, 12–13 precaudal, 20–22 caudal.

Types of Nominal Species: *Trigla lucerna* Linnaeus. Holotype BMNH 1853.11.12:16, 221 mm (WHEELER, 1958). I did not examine this specimen, but a photograph of it supplied by ALWYNNE C. WHEELER is presented in Plate VII B.

Trigla hirundo Linnaeus. Apparently no types extant.

Other type specimens not examined.

Distribution: From Norway and the North Sea south along the Atlantic coast of Europe, around the British Isles, in the Mediterranean, and in the Black Sea (SVETOVIDOV, 1936). *C. lucernus* (SVETOVIDOV, 1936) has been reported from Cape Verde (CADENAT, 1950); records of its presence from farther south in the Gulf of Guinea and Angola probably based on specimens of either *C. gabonensis* or *C. capensis*, or both.

Discussion: Meristic characters are shown for this species in Tables 1, 2, and 3 (pp. 112–113). *C. lucernus* is most closely related to *C. capensis* of South Africa and to the Indo-Pacific species *C. kumu* (Lesson and Garnot) and *C. spinosus* (McClelland). These four species are, in turn, related to *C. gabonensis* and the South African *C. queketti* (Regan).

Chelidonichthys* (*C.*) *capensis (Cuvier *in* CUVIER & VALENCIENNES)

(Fig. 8)

Trigla capensis Cuvier *in* CUVIER & VALENCIENNES, 1829: 55 (original description; Cape of Good Hope).

Material:

ANSP: 103651, Delagoa Bay, Mocambique, 1946.—1(226).

"Galathea":

ZMUC: P79982–83, St. 139, Walvis Bay, South West Africa, 24.12.1950.—2(165–182).

Diagnosis: A species of *Chelidonichthys* closely related to *C. lucernus* but having accessory branches on the swimbladder; breast naked and belly partially scaled; embedded body scales, 19–21 above lateral line and 47–48 below lateral line (diagonal count); 33–34 vertebrae, 12–13 precaudal and 21 caudal.

Distribution: This is a South African species (SMITH, 1961), which ranges northward in the Atlantic to Walvis Bay (SMITH, 1966)—see Fig. 2.

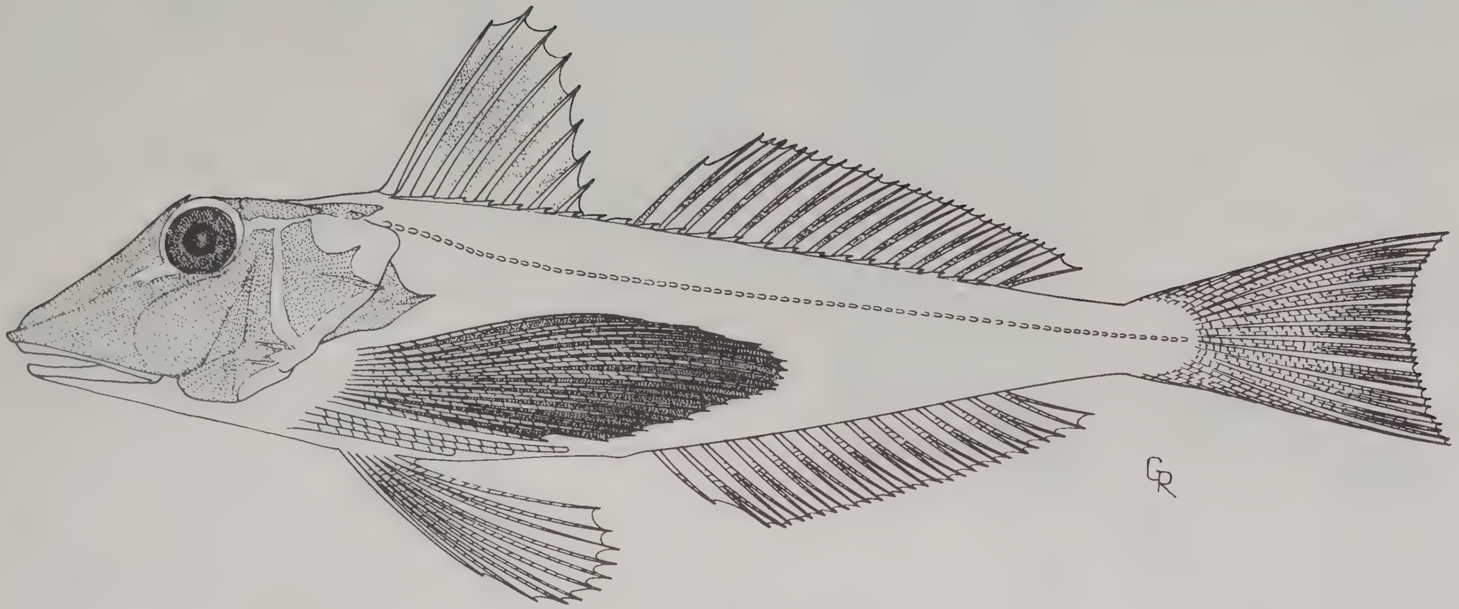

Fig. 8. *Chelidonichthys capensis* (Cuvier *in* CUVIER & VALENCIENNES). ZMUC P79982, Walvis Bay, South West Africa, 182 mm SL.

Discussion: Meristic characters for this species appear in Table 1, 2, and 3 (pp. 112–113). *C. capensis* is a member of the *lucernus-kumu-spinosus* species group. It has been synonymized with *lucernus* by various authors (cf. Svetovidov, 1936), but I consider it a valid species separate from *lucernus;* Smith (1961) has shown it to be distinct from *kumu*.

Chelidonichthys (C.) gabonensis (Poll & Roux)

(Fig. 9)

Trigla gabonensis Poll & Roux, 1955: 1 (original description; Gulf of Guinea).
Chelidonichthys senegalensis Puyo, 1957: 182 (original description; Senegal).

Material:
"Atlantide":
ZMUC: P79984–85, St. 70, 4°50′N, 2°49′W, 60 m, 15.1.1946.—2(90–136).
P79986–98, St. 123, 2°03′S, 9°05′E, 49 m, 5.3.1946.—13(116–142).
P79999, St. 133, 7°19′S, 12°40′E, 47 m, 16.3.1946.—1(61).

"Geronimo":
TABL: 101041, Cruise 2, St. 189, 1°00′S, 8°29′E, 100 m, 2.9.1963.— 4(152–206).
101042, Cruise 2, St. 191, 1°18′S, 8°41′E, 38 m, 2.9.1963.—12(135–167).
101043, Cruise 2, St. 202, 2°00′S, 8°55′E, 100 m, 4.9.1963.—1(175).
101044, Cruise 2, St. 211, 2°32′S, 9°05′E, 100 m, 5.9.1963.—2(125–160).
101045, Cruise 2, St. 218, 3°01′S, 9°24′E, 100 m, 6.9.1963.—2(45–49).
101046, Cruise 2, St. 235, 4°00′S, 10°35′E, 100 m, 8.9.1963.—2(190–205).

"Guinean Trawling Survey I":
USNM: 201780, Transect 4, St. 2, 10°29′N, 16°20′W, 30 m, 5.12.1963.—8(157–193).
201781, Transect 5, St. 4, 9°47′N, 16°02′W, 50 m, 1.12.1963.—1(159).
201782, Transect 8, St. 4, 8°34′N, 14°14′W, 50 m, 25.11.1963.—4(152–170).
201808, Transect 8, St. 5, 8°32′N, 14°17′W, 70 m, 25.11.1963.—1(157).
201783, Transect 9, St. 5, 7°50′N, 14°00′W, 70 m, 20.11.1963.—5(149–166).
201784, Transect 17, St. 2, 4°56′N, 9°00′W, 30 m, 1.11.1963.—1(130).
201785, Transect 17, St. 3, 4°55′N, 9°00′30″W, 40 m, 1.11.1963.—2(65–122).
201786, Transect 18, St. 4, 4°35′N, 8°25′30″W, 50 m, 30.10.1963.—8(71–157).
201787, Transect 18, St. 6, 4°28′N, 8°28′30″W, 100 m, 31.10.1963.—6(137–176).
Transect 29, St. 4B, 4°41′N, 1°36′W, 51 m, 19.9.1963.—2(133–146).
Transect 30, St. 4N, 4°41′N, 0°57′W, 50 m, 22.9.1963.—2(127–136).
Transect 30, St. 5B, 4°36′N, 0°53′W, 71 m, 22.9.1963.—1(170).

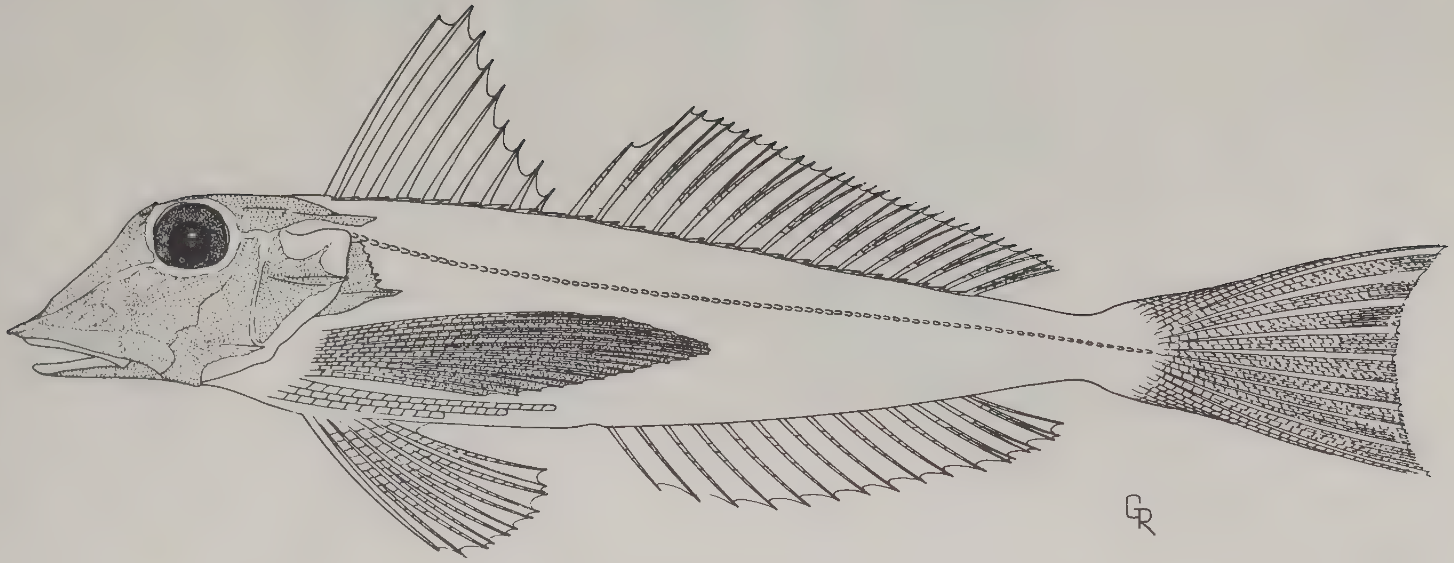

Fig.9. *Chelidonichthys gabonensis* (Poll & Roux). TABL 101046, Gulf of Guinea, “Geronimo” Cruise 2, St. 235, 4°00′S, 10°35′E, 190 mm SL.

"Guinean Trawling Survey II":
Transect 53, St. 3, 0°12′S, 9°04′E, 40 m, 9.5.1964.—2(152–159).
Transect 62, St. 5, 5°17′S, 11°46′E, 70 m, 24.5.1964.—1(227).

"Pillsbury":
UMML: 15250, St. 64, 4°23′N, 7°06.5′W, 2.6.1964.—2(106–109).
15768, St. 65, 4°15′N, 7°32′W, 2.6.1964.—6(108–188).
15861, St. 17, 5°35′N, 0°10′E, 26.5.1964.—1(147).
16406, St. 30, 4°46′N, 2°30′W, 28.5.1964.—1(117).
16595, St. 32, 4°37′N, 2°32′W, 28.5.1964.—1(189).
16790, St. 30, 4°46′N, 2°30′W, 28.5.1964.—1(142).

Diagnosis: A species of *Chelidonichthys* with normal lateral-line scales lacking spines or platelike expansions; swimbladder with no accessory branches; breast and belly fully scaled; body scales not deeply embedded, deciduous in preserved specimens, with 8–12 above lateral line and 27–35 below lateral line (diagonal count); 33–34 vertebrae, 12–13 precaudal, and 20–22 caudal.

Types of Nominal Species: *Trigla gabonensis* Poll & Roux. Types not examined. *Chelidonichthys senegalensis* Puyo. Types apparently not extant (M. L. BAUCHOT, personal communication).

Distribution: *C. gabonensis* is endemic to the Gulf of Guinea, from Cape Verde, Senegal, south to latitude 14°05′S (POLL, 1959). It is also reported off Angola by SANCHES (1966) (Fig. 2).

Discussion: This species is closely related to the South African *C. queketti* (Regan). As is true of *C. lastoviza* and *C. africanus*, many more specimens from both areas must be acquired and studied to determine their status. Meristic characters for *C. gabonensis* are shown in Tables 1, 2, and 3 (pp. 112–113).

Ecologically this species was found on the continental shelf waters between 30 and 100 m deep. At "Geronimo" St. 191 (38 m deep), bottom temperature was 18.5°C, salinity was $36.0\,^0/_{00}$, and dissolved oxygen was 3.44 ml/L. At the four other "Geronimo" stations the depth was 100 m, temperature ranged from 15.7 to 16.5°C, salinity ranged from $35.6\,^0/_{00}$ to $35.8\,^0/_{00}$, and dissolved oxygen measured from 1.95 to 3.17 ml/L.

Lepidotrigla cavillone (Lacépède)

(Fig. 10)

Trigla cavillone Lacépède, 1802: 341, 366 (original description; French coast of the Mediterranean).

Trigla aspera Viviani, 1805 (original description *fide* CUVIER *in* CUVIER & VALENCIENNES 1829, p. 77, the species described and attributed to VIVIANI.)

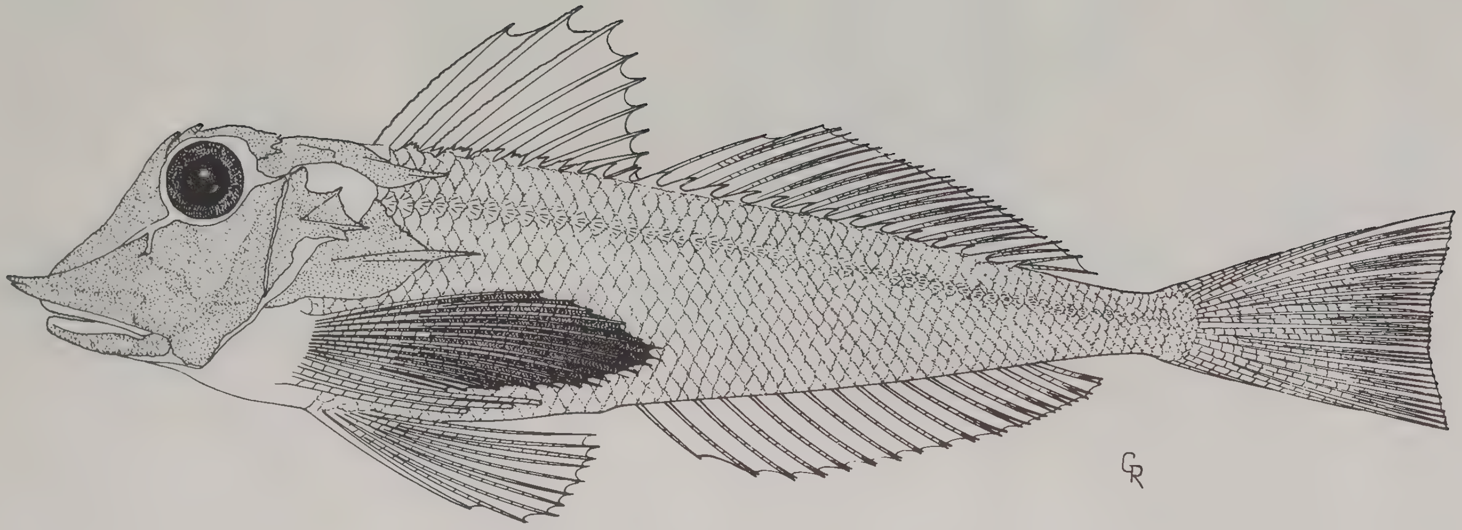

Fig. 10. *Lepidotrigla cavillone* (Lacépède). TABL 101040, Naples, Italy, 132 mm SL.

Trigla gonotus Rafinesque, 1810: 32 (original description; Sicily).
Trigla leucoptera Swainson, 1838: 422 (original description; Sicily).

Material:
ANSP: 11718–31, Mediterranean, Bonaparte Collection No. 102,—1(95).
11784–800, Mediterranean, Bonaparte Collection No. 95,—18(49–82).
SU: 1317, Venice, Italy.—5(79–85).
1391, Naples, Italy.—1(85).
2388, Venice, Italy.—2(91–100).
ZMUC: P791000, Morocco.—1(86).
TABL.: 101040, Cuma Beach Near Pozzuoli, Naples, Italy, 15–20 m, 21–22.7.1966. —12(88–133).

Diagnosis: A species of *Lepidotrigla* with first dorsal spine serrate anteriorly; scaleless breast; cleithral spine long, greater than 13% SL; body scales firmly attached; 30–32 vertebrae, 11–13 precaudal, 19–21 caudal.

Distribution: This species is primarily Mediterranean, but MURRAY & HJORT (1912) recorded it at stations between Gibraltar and the Canary Islands and between the Canary Islands and Cape Bojados, Spanish West Africa.

Discussion: Meristic characters are shown in Tables 1, 2, and 3 (pp. 112–113) and the relationship between *L. cavillone* and *L. carolae* is discussed in the account of *L. carolae*.

Lepidotrigla cadmani Regan

(Fig. 11)

Lepidotrigla cadmani Regan, 1915: 128 (original description; Lagos, Nigeria).
Lepidotrigla laevispinnis Blache & Ducroz, 1960: 205 (original description; Pointe Noire, République du Congo).

Material:
SU: 15951, Kribi, Cameroon, 9.4.1940,—1(136).
BMNH: 1914.11.2:51, off Lagos, Nigeria, 2.11.1914,—1(133).
1914.11.2:52–53, off Lagos, Nigeria, 2.11.1914,—2(109–118).

"Atlantide":
ZMUC: P791001–4, St. 70, 4°50′N, 2°49′W, 60 m, 15.1.1946.—4(115–130).
P791005–12, St. 85, 5°37′N, 0°38′E, 28–40 m, 30.1.1946.—8(30–117).
P791013, St. 96, off Lagos, Nigeria, 40–51 m, 14.2.1946.—1(25).
P791014–20, St. 103, 4°38′N, 5°19′E, 40 m, 17.2.1946.—7(30–45).
P791021–25, St. 106, 3°55′N, 6°08′E, 55–88 m, 18.2.1946.—5(99–125).

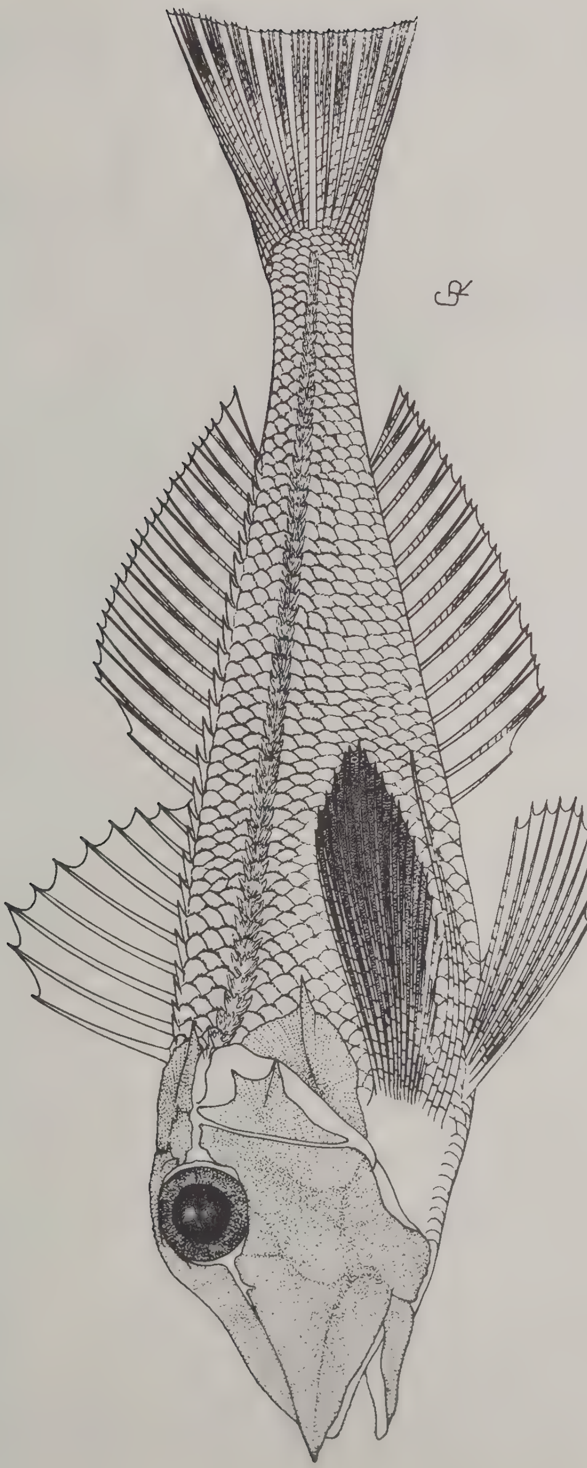

Fig. 11. *Lepidotrigla cadmani*
Regan. TABL 101056, Gulf of
Guinea, "Geronimo" Cruise 2,
St. 179, 0°02′S, 8°50′E,
150 mm SL.

P791026–27, St. 116, 4°01′N, 7°56′E, 23.2.1946.—2(99–113).
P791028–31, St. 120, 2°09′N, 9°27′E, 260–850 m, 1.3.1946.—4(107–141).
P791032, St. 145, 9°20′N, 14°15′E, 32 m, 13.4.1946.—1(75).

"Geronimo":
TABL: 101055, Cruise 2, St. 177, 0°01′S, 8°55′E, 100 m, 31.8.1963.—7(105–120).
101056, Cruise 2, St. 179, 0°02′S, 8°50′E, 295 m, 31.8.1963.—1(150).
101057, Cruise 2, St. 189, 1°00′S, 8°29′E, 100 m, 2.9.1963.—10(110–140).
101058, Cruise 2, St. 196, 1°30′S, 8°37′E, 100 m, 3.9.1963.—4(111–124).
101059, Cruise 2, St. 197, 1°30′S, 8°27′E, 200 m, 3.9.1963.—4(125–143).
101060, Cruise 2, St. 202, 2°00′S, 8°55′E, 100 m, 4.9.1963.—3(117–142).
101061, Cruise 2, St. 203, 2°01′S, 8°50′E, 200 m, 4.9.1963.—5(135–145).
101062, Cruise 2, St. 211, 2°32′S, 9°05′E, 100 m, 5.9.1963.—5(105–135).
101063, Cruise 2, St. 212, 2°30′S, 8°58′E, 200 m, 5.9.1963.—3(125–137).
101064, Cruise 2, St. 219, 3°01′S, 9°22′E, 200 m, 6.9.1963.—2(125–155).
101065, Cruise 2, St. 227, 3°30′S, 8°53′E, 200 m, 7.9.1963.—5(125–150).
101066, Cruise 2, St. 228, 3°31′S, 9°53′E, 400 m, 7.9.1963.—2(115–125).
101067, Cruise 2, St. 236, 4°03′S, 10°22′E, 200 m, 8.9.1963.—5(115–145).
101068, Cruise 2, St. 245, 4°31′S, 10°54′E, 200 m, 9.9.1963.—1(160).
101069, Cruise 2, St. 251, 4°17.5′N, 1°41′W, 16.9.1963.—2(135–140).

"Guinean Trawling Survey I":
USNM: 201788, Transect 1, St. 5, 12°08′N, 17°14′W, 70 m, 12.12.1963.—11(111–130).
201789, Transect 2, St. 4, 11°32′N, 17°11′W, 50 m, 10.12.1963.—8(63–90).
201790, Transect 3, St. 7, 10°44′N, 17°06′W, 200 m, 8.12.1963.—7(110–137).
201791, Transect 15, St. 6, 5°43′N, 10°22.5′W, 100 m, 6.11.1963.—1(133).
201792, Transect 16, St. 4, 5°28.5′N, 9°46′W, 50 m, 3.11.1963.—15(110–128).
201793, Transect 17, St. 3, 4°55′N, 9°00.5′W, 42 m, 1.11.1963.—9(81–132).
201794, Transect 17, St. 6, 4°40′N, 9°11′W, 98–102 m, 2.11.1963.—5(115–128).
201795, Transect 18, St. 4,, 4°35′N, 8°25.5′W, 50–52 m, 30.10.1963.—2(119–125).
201796, Transect 18, St. 6, 4°28′N, 8°28.5′W, 100 m, 31.10.1963.—2(119–126).
Transect 30, St. 5B, 4°36′N, 0°53′W, 71 m, 22.9.1963.—1(105).

"Pillsbury":
UMML: 15674,St. 29, 4°38′N, 2°02′W, 28.5.1964.—9(107–136).
15999, St. 45, 5°05′N, 4°04.5′W, 30.5.1964.—3(143–163).
16425, St. 24, 4°56′N, 0°47.5′W, 28.5.1964.—1(40).
16592, St. 32, 4°37′N, 2°32′W, 28.5.1964.—2(131–141).
16742, St. 68, 4°23′N, 8°05.5′W, 3.6.1964.—1(113).

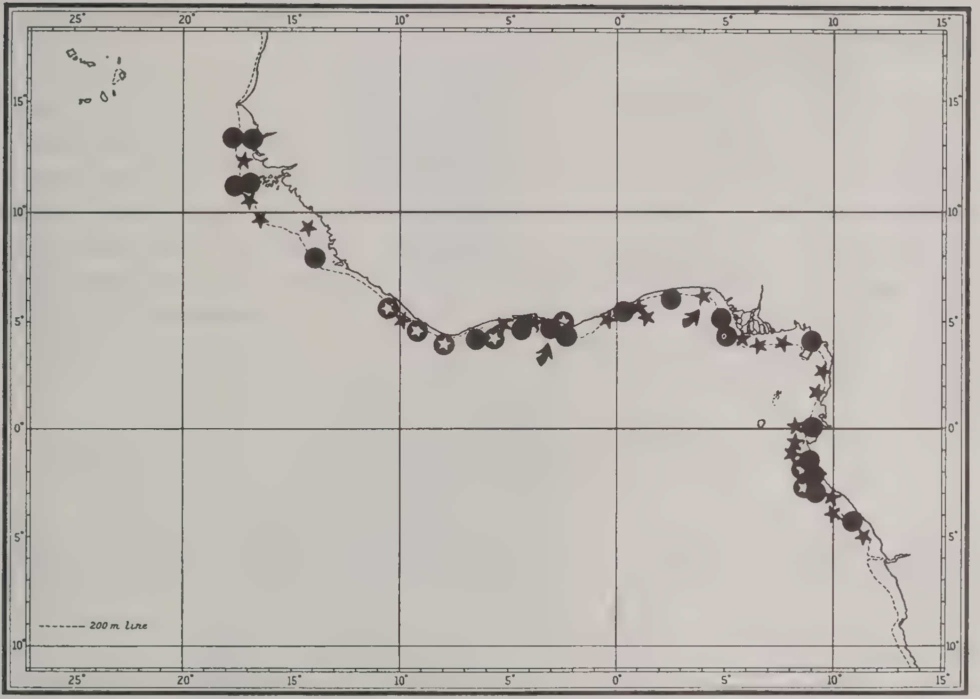

Fig. 12. Distribution of *Lepidotrigla carolae* (circles), *L. cadmani* (stars), and both species (circled stars), in the tropical eastern Atlantic based on specimens examined. Type localities denoted by arrows.

16785, St. 30, 4°46′N, 2°30′W, 28.5.1964.—1(76).
16884, St. 83, 4°59′N, 9°37′W, 5.6.1964.—2(115–125).
16998, St. 50, 4°58′N, 5°00′W, 31.5.1964.—1(17).
17811, St. 68, 4°23′N, 8°05′W, 3.6.1964.—1(115).
17812, St. 59, 4°57′N, 5°22′W, 1.6.1964.—1(157).
17813, St. 13, 6°08′N, 2°09′W, 26.5.1964.—1(99).
17814, St. 32, 4°37′N, 2°32′W, 28.5.1964.—1(129).
21485, St. 241, 4°35′N, 5°18′E, 13.5.1965.—5(52–116).

Diagnosis: A species of *Lepidotrigla* with first dorsal spine smooth anteriorly; breast scaly; 29–31 vertebrae, 10–12 precaudal, 18–19 caudal.

Types of Nominal Species: *Lepidotrigla cadmani* Regan. Lectotype BMNH 1914.11.2:51, ♂ 132.7 mm SL, off Lagos, Nigeria in 10–35 fathoms, 2 November 1914, herein selected. REGAN based his description on five specimens collected together in the Gulf of Guinea off Lagos, Nigeria. I examined two of the remaining four paralectotypes (BMNH 1914.11.2:52–53).

Lepidotrigla laevispinnis Blache & Ducroz. Types not examined.

Distribution: Endemic to the Gulf of Guinea from Senegal (CADENAT, 1950) to Angola (SANCHES, 1966)—see Fig. 12.

Discussion: Meristic characters of this species are presented in Tables 1, 2, and 3 (pp. 112–113). *L. cadmani* is easily separable from *L. cavillone* and *L. carolae* and apparently belongs to a different species group of this principally Indo-Pacific genus.

L. cadmani and *L. carolae* are the most abundant and ecologically wide-ranging gurnards in the Gulf of Guinea. Specimens of *L. cadmani* have been collected at depths from 30 m to as deep as 400 m. At 13 "Geronimo" stations from which specimens were taken, depths ranged from 100 to 400 m, temperature from 10.0 to 16.5 °C, salinity from $34.9^{0}/_{00}$ to $35.8^{0}/_{00}$, and dissolved oxygen from 1.40 to 3.27 ml/L.

Lepidotrigla carolae n. sp.

(Fig. 13)

Holotype: ZMUC P791033, (♂, 90.5), Gulf of Guinea, "Atlantide" St. 70, 04°50′N, 2°49′W, 15 January 1946, 60 m.

Paratypes:
"Atlantide":
ZMUC: P791034–35, St. 61, 4°57′N, 9°26′W, 9.1.1946.—2(91–94).
P791036–39, St. 68, 4°38′N, 6°18′W, 90 m, 12.1.1946.—4(86–94).
P791040–47, St. 70, 4°50′N, 2°49′W, 60 m, 15.1.1946.—8(65–97).
P791048–49, St. 123, 2°03′S, 9°05′E, 49 m, 5.3.1946.—2(75–77).
P791050–52, St. 161, off Bathhurst, Gambia, 24.4.1946.—3(24–90).
P791053–56, St. 163, 13°43′N, 17°23′W, 76–89 m, 25.4.1946.—4(87–96).

"Geronimo":
ANSP: 109214, Cruise 2, St. 202, 2°00′S, 8°55′E, 100 m, 4.9.1963.—2(78–90).
BMNH: 1967.7.24.1–2, Cruise 2, St. 212, 2°30′S, 8°58′E, 200 m, 5.9.1963.—2(95–98).
TABL: 101070, Cruise 2, St. 177, 0°01′S, 8°55′E, 100 m, 31.8.1963.—5(95–105).
101071, Cruise 2, St. 194, 1°18′S, 8°23′E, 128 m, 2.9.1963.—1(112).
101072, Cruise 2, St. 196, 1°30′S, 8°37′E, 100 m, 3.9.1963.—8(90–95).
101073, Cruise 2, St. 210, 2°30′S, 9°04′E, 100 m, 5.9.1963.—4(76–95).
101074, Cruise 2, St. 218, 3°01′S, 9°24′E, 100 m, 6.9.1963.—3(26–34).
101075, Cruise 2, St. 227, 3°30′S, 8°53′E, 200 m, 7.9.1963.—10(87–93).
101076, Cruise 2, St. 235, 4°00′S, 10°35′E, 100 m, 8.9.1963.—5(30–78).
101077, Cruise 2, St. 251, 4°17.5′N, 1°41′W, 16.9.1963.—10(90–95).

"Guinean Trawling Survey I":
USNM: 201725, Transect 2, St. 4, 11°32′N, 17°11′W, 50 m, 10.12.1963.—1(59).
201726, Transect 2, St. 5, 11°28′N, 17°17′W, 70 m, 10.12.1963.—19(79–96).
201727, Transect 9, St. 5, 7°50′N, 14°00′W, 70 m, 20.11.1963.—5(89–99).

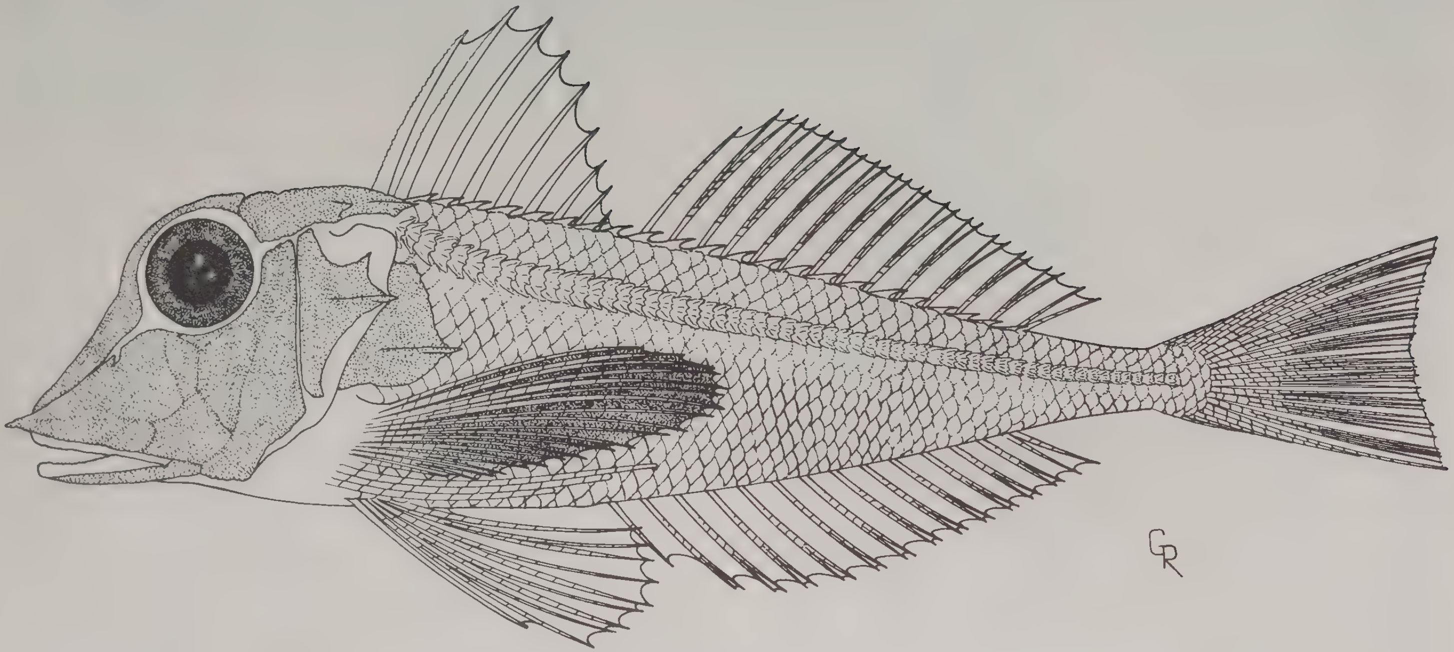

Fig. 13. *Lepidotrigla carolae* n. sp.
Holotype ZMUC P791033,
Gulf of Guinea, "Atlantide"
St. 70, 4°50′N, 2°49′W, 91 mm SL.

201728, Transect 15, St. 6, 5°43′N, 10°22′W, 100 m, 6.11.1963.—1(101).
201729, Transect 17, St. 5, 4°48′N, 9°05′W, 70 m, 2.11.1963.—11(79–93).
201730, Transect 17, St. 6, 4°40′N, 9°11′W, 98–102 m, 2.11.1963.—7(87–102).

"Pillsbury":
UMML: 15251, St. 64, 4°23′N, 7°06.5′W, 2.6.1964.—6(67–77).
16006, 5°05′N, 4°04.5′W, 30.5.1964.—2(100–105).
16337, 6°08′N, 2°09′E, 26.5.1964.—2(57–62).
16404, St. 30, 4°46′N, 2°30′W, 28.5.1964.—1(45).
16592, St. 32, 4°37′N, 2°32′W, 28.5.1964.—3(37–114).
16742, St. 68, 4°23′N, 8°05.5′W, 3.6.1964.—1(89).
16827, St. 22, 5°25′N, 0°01′W, 27.5.1964.—1(95).
17010, 4°57′N, 5°22′W, 1.6.1964.—1(83).
21313, St. 245, 4°32′N, 5°07′E, 64–119 m, 13.5.1965.—9(49–86).
21371, St. 236, 5°20′N, 4°45′E, 101–128 m, 12.5.1965.—6(82–95).
21463, St. 232, 5°56′N, 4°27′E, 11.5.1965.—7(84–102).
21537, St. 237, 5°19′N, 4°48′E, 12.5.1965.—3(87–101).
21577, St. 259, 3°53′N, 8°53′E, 16.5.1965.—3(25–31).
21587, St. 239, 4°56′N, 5°00′E, 13.5.1965.—9(50–93).

Diagnosis: A species of *Lepidotrigla* with first dorsal spine serrate anteriorly; breast scaleless; cleithral spine short, less than 13% SL; body scales deciduous; 30–32 vertebrae, 10–12 precaudal, 19–22 caudal.

Description: Measurements for the holotype and paratypes are given in Table 4 (p. 114). Meristic characters are given in Tables 1, 2, and 3. This species is small (largest specimen examined was 114 mm SL), with deep head and body; preorbital spines vary in length, size, and number, one to three usually pronounced; nuchal spines extend slightly beyond dorsal fin origin; opercular spine short, extending only slightly beyond opercular membrane; bucklers along base of dorsal fin strong, with one spine on each unit; cleithral or humeral spine strong. Bony lateral-line scales with six to seven pores anteriorly reduced to three on caudal peduncle; ctenoid body scales above lateral line, on nape and one to three rows below lateral line; slightly ctenoid scales on flanks; cycloid scales on lower flanks and belly; breast naked; cycloid scales loosely held and lost from most specimens. Anterior edge of first dorsal spine serrated, remaining spines smooth. Pectoral fin extends beyond anal origin, pelvic fin reaches anal origin. Prevomerine teeth present. In life, body and head mainly red with white breast, belly, and lower flanks; preserved specimens brown except for white breast, occasionally white on belly and flanks; first dorsal fin with posterior black spot; caudal fin with dusky vertical bar.

Distribution: Similar to *L. cadmani* from Senegal to Angola. Material examined was from latitude 13°43′N to 4°00′S (Fig. 12).

Discussion: This species is closely related to *L. cavillone* and separable from it by the characters noted above. *L. carolae* is sympatric with, but easily separable from, *L. cadmani* with which it has been confused.

Specimens of *L. carolae* have been collected at depths from 49 m to as deep as 200 m. At 10 "Geronimo" stations from which specimens were taken, depths ranged from 100 to 200 m, temperature from 14.0 to 16.7 °C, salinity from 35.4 ‰ to 36.0 ‰, and dissolved oxygen from 1.95 to 3.80 ml/L.

Etymology: This species is named for my wife, Carol.

SUMMARY

Accounts are given for the eleven species of three genera of gurnards known from the eastern Atlantic Ocean. Of these, two species range from northern Europe southward to Angola, five are found only in European and North African waters, three are endemic species of the Gulf of Guinea (one of which is described here as new), and one South African species ranges northward to Angola. The confused nomenclature of the European species is analysed and the following are names applicable to these seven species: *Trigla lyra* Linnaeus, *Chelidonichthys lastoviza* (Bonnaterre), *C. gurnardus* (Linnaeus), *C. obscurus* (Bloch and Schneider), *C. lucernus* (Linnaeus), *C. cuculus* (Linnaeus), and *Lepidotrigla cavillone* (Lacépède).

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ADDENDUM

Two papers recently came to my attention, which described, but regrettably, did not name a new species of *Lepoditrigla* from the Mediterranean Sea (Audouin, J. 1965: Contribution a l'étude des poissons du genre *Lepidotrigla* des côtes occidentales de l'Algérie. Comm. Int. Explor. Sci. Médit. Rapp. et P. V. Res. **18** (2): 265–266. Duclerc, Jean 1967: Un triglidé nouveau pour les côtes françaises de Méditerranée. Rev. Trav. Inst. Pêches Marit. **31** (4): 363–365).

None of the specimens I examined were of this new species; from the descriptions presented in the two papers, I have no doubt that this new species is indeed valid. Based on the characters presented, the unnamed species is probably closely related to *L. cadmani*. A comparison of the two would be helpful.

Duclerc presented a key for separating *L. cavillone* from the new species, translated as follows:

Spines present on the supra-orbital and on the edge of the nuchal ridge, vertical diameter of the eye less than the distance to the lower edge of the orbital base of the mandible, adherent scales distinctly ctenoid and higher than broad..*L. cavillone*

Orbital and nuchal spines absent, vertical diameter of the eye equal to or greater than the distance from the lower edge to the orbital base of the mandible, less adherent scales which are weakly ctenoid and broader than high . . . .*L. sp.*

Table 1. Number of dorsal spines, dorsal soft rays, anal rays, and dorsal bucklers in eastern Atlantic gurnards.
(Holotype, neotype, and lectotype indicated in boldface).

	Dorsal spines						Dorsal rays								
	8	9	10	11	N	x̄	13	14	15	16	17	18	19	N	x̄
T. lyra	1	36	8	–	45	9.16	–	–	33	12	–	–	–	45	15.27
C. lucernus	4	17	2	–	23	8.91	–	–	–	20	3	–	–	23	16.13
C. capensis	1	2	–	–	3	8.67	–	–	2	1	–	–	–	3	15.33
C. gabonensis	–	17	58	–	75	9.77	–	–	15	57	3	–	–	75	15.84
C. lastoviza	–	3	40	5	48	10.04	–	–	2	39	6	–	–	47	16.08
C. gurnardus	8	2	–	–	10	8.20	–	–	–	–	–	–	7	7	19.00
C. obscurus	–	–	7	4	11	11.36	–	–	–	–	1	8	2	11	18.09
C. cuculus	–	**6**	1	–	7	9.14	–	–	–	–	**3**	4	–	7	17.57
L. cavillone	2	22	–	–	24	8.92	–	2	20	3	–	–	–	25	15.04
L. carolae	15	**67**	–	–	82	8.82	–	**14**	59	4	–	–	–	77	14.87
L. cadmani	3	**50**	1	–	54	8.96	3	**49**	2	–	–	–	–	54	13.98

	Anal rays									Dorsal bucklers									
	13	14	15	16	17	18	19	N	x̄	21	22	23	24	25	26	27	28	N	x̄
T. lyra	–	–	22	23	–	–	–	45	15.51	–	–	1	36	8	–	–	–	45	24.16
C. lucernus	–	1	14	8	–	–	–	23	15.30	–	–	–	2	20	1	–	–	23	24.96
C. capensis	–	1	2	–	–	–	–	3	14.67	–	–	1	1	1	–	–	-	3	24.00
C. gabonensis	–	6	66	3	–	–	–	75	14.96	–	–	–	19	53	3	–	–	75	24.79
C. lastoviza	–	–	16	28	3	–	–	47	15.72	–	–	–	–	41	6	–	–	47	25.13
C. gurnardus	–	–	–	–	–	4	5	9	18.56	–	–	–	–	–	–	3	9	12	27.75
C. obscurus	–	–	–	–	6	5	–	11	17.45	–	–	–	–	–	1	10	–	11	26.99
C. cuculus	–	–	–	**4**	1	2	–	7	16.71	–	–	–	–	–	1	**10**	–	11	26.99
L. cavillone	1	5	15	4	–	–	–	25	14.88	–	5	17	3	–	–	–	–	25	22.92
L. carolae	–	11	**65**	4	–	–	–	80	14.91	–	**16**	58	5	–	–	–	–	79	22.86
L. cadmani	5	**47**	3	–	–	–	–	55	13.96	5	**45**	5	–	–	–	–	–	55	22.00

Table 2. Total number of gill rakers on the first arch excluding rudiments, in eastern Atlantic gurnards.
(Holotype, neotype, and lectotype indicated in boldface).

	Total gill rakers																	
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	N	x̄
T. lyra	–	–	–	6	13	18	4	3	–	–	–	–	–	–	–	–	44	8.66
C. lucernus	–	–	–	4	9	7	2	1	–	–	–	–	–	–	–	–	23	8.91
C. capensis	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	–	3	16.67
C. gabonensis	–	1	17	47	10	–	–	–	–	–	–	–	–	–	–	–	75	6.88
C. lastoviza	5	3	17	11	7	–	–	–	–	–	–	–	–	–	–	–	42	6.43
C. gurnardus	–	–	–	–	–	–	1	–	1	3	2	–	–	–	–	–	7	12.71
C. obscurus	–	–	-	1	–	2	6	2	–	–	–	–	–	–	–	–	11	9.73
C. cuculus	–	–	–	1	**1**	1	1	1	–	–	–	–	–	–	–	–	5	9.00
L. cavillone	–	4	10	8	2	1	–	–	–	–	–	–	–	–	–	–	25	6.44
L. carolae	2	9	36	**13**	–	–	–	–	–	–	–	–	–	–	–	–	60	6.00
*L. cadmani**	4	7	**8**	7	6	11	2	–	–	–	–	–	–	–	–	–	45	7.00

* All gill rakers rudimentary.

Table. 3. Number of precaudal, caudal, and total vertebrae in the eastern Atlantic Triglidae. (Holotype, neotype, and lectotype indicated in bold face).

	Precaudal							Caudal											
	10	11	12	13	14	N	x̄	18	19	20	21	22	23	24	25	26	27	N	x̄
T. lyra	–	2	8	–	–	10	11.80	–	2	7	1	–	–	–	–	–	–	10	19.90
C. lucernus	–	–	7	16	–	23	12.70	–	–	1	16	6	–	–	–	–	–	23	21.22
C. capensis	–	–	2	1	–	3	12.33	–	–	–	3	–	–	–	–	–	–	3	21.00
C. gabonensis	–	–	6	4	–	10	12.40	–	–	1	3	6	–	–	–	–	–	10	21.50
C. lastoviza	–	–	2	19	10	31	13.26	–	–	2	20	9	–	–	–	–	–	31	21.22
C. gurnardus	–	1	4	1	–	6	12.00	–	–	–	–	–	–	–	1	4	1	6	26.00
C. obscurus	–	–	6	5	–	11	12.45	–	–	–	–	–	3	8	–	–	–	11	23.73
C. cuculus	–	–	–	1	**4**	5	13.80	–	–	–	–	3	2	–	–	–	–	5	22.40
L. cavillone	–	19	5	1	–	25	11.28	–	5	14	6	–	–	–	–	–	–	25	20.04
L. carolae	**4**	29	2	–	–	35	10.94	–	5	**28**	1	1	–	–	–	–	–	35	19.94
L. cadmani	1	**12**	3	–	–	16	11.12	3	**13**	–	–	–	–	–	–	–	–	16	18.81

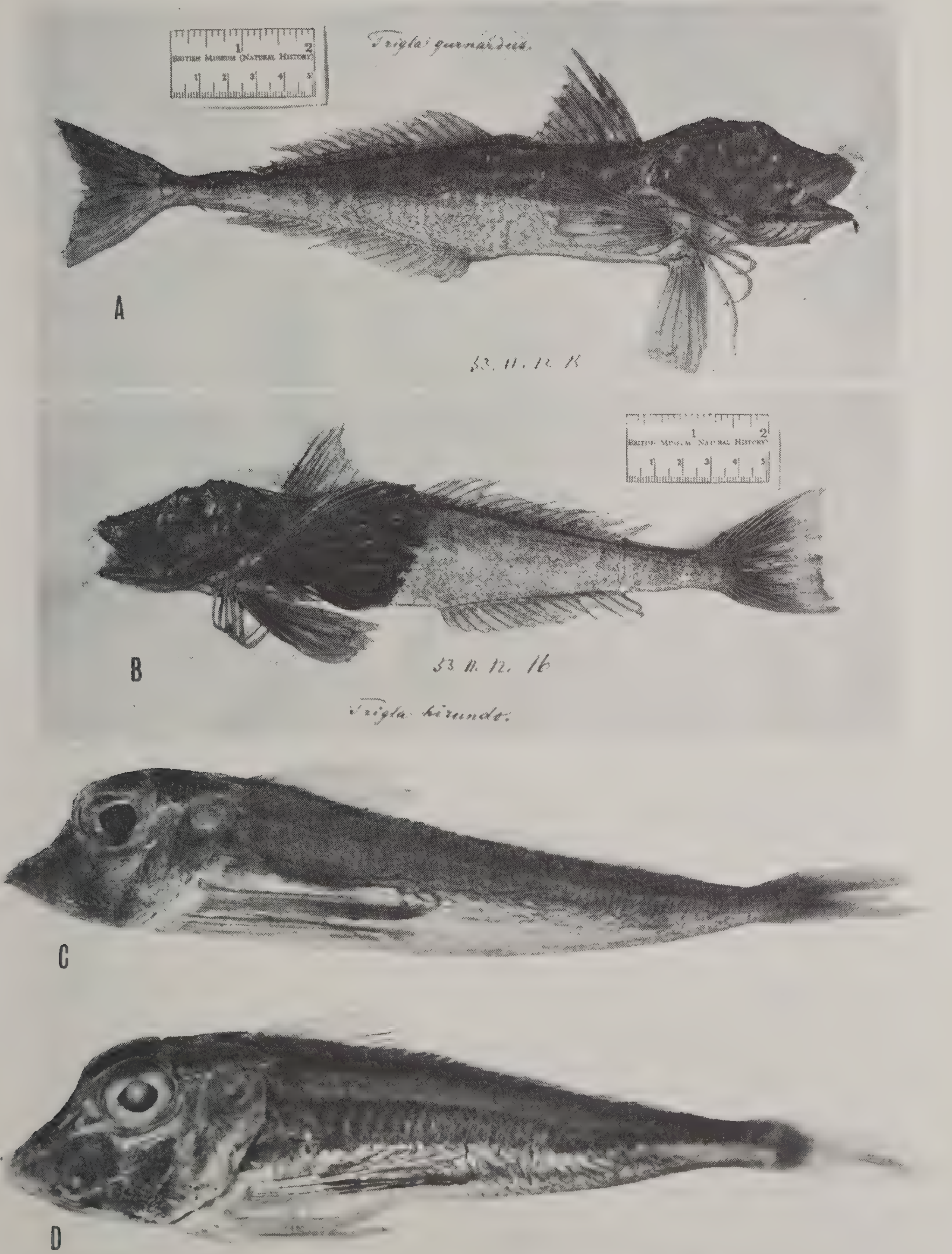
	Total												
	29	30	31	32	33	34	35	36	37	38	39	N	x̄
T. lyra	–	–	3	7	–	–	–	–	–	–	–	10	31.70
C. lucernus	–	–	–	–	2	21	–	–	–	–	–	23	33.91
C. capensis	–	–	–	–	2	1	–	–	–	–	–	3	33.33
C. gabonensis	–	–	–	–	1	9	–	–	–	–	–	10	33.90
C. lastoviza	–	–	–	–	2	12	17	–	–	–	–	31	34.48
C. gurnardus	–	–	–	–	–	–	–	–	1	4	1	6	38.00
C. obscurus	–	–	–	–	–	–	–	9	2	–	–	11	36.18
C. cuculus	–	–	–	–	–	–	–	**4**	1	–	–	5	36.20
L. cavillone	–	2	13	10	–	–	–	–	–	–	–	25	31.32
L. carolae	–	**7**	25	3	–	–	–	–	–	–	–	35	30.88
L. cadmani	1	**14**	1	–	–	–	–	–	–	–	–	16	30.00

ADDITION TO ADDENDUM SECTION

The results of the Guinean Trawling Survey (F. WILLIAMS, 1968: Report on the Guinean Trawling Survey.—Vol. 1. General Report. Organisation of African Unity Scientific, Technical and Research Commission, Lagos, Nigeria) has just been published. Although I have not had the opportunity to study this report in detail, the predictable widespread use of this work necessitates brief comment here. In Tables 847 and 848 (p. 595), WILLIAMS lists 10 gurnards. His *Peristedion cataphractum* was not considered by me since I place that species in the family Peristediidae: *Lepidotrigla cadmani* is referable to *L. carolae; L. laevispinnis* is referable to *L. cadmani; Lepidotrigla* spp. refers to either species; *Trigla lineata* is referable to *Chelidonichthys lastoviza; T. hirundo* and *T. lucerna* are probably both referable to *T. gabonensis* (= *C. gabonensis*); *T. lyra* is not questionable; and *Trigla* spp. is most likely referable to *C. gabonensis*.

Table 4. Selected measurements of *Lepidotrigla carolae* type specimens expressed as ranges in percentage of standard lenght.

Measurement	Holotype	6 Paratypes	32 Paratypes	26 Paratypes
Standard length (mm)	90.5	24.2–34.2	57.2–89.7	90.8–101.7
Head length	33.0	24.4–40.3	25.1–35.6	29.9–34.8
Length of orbit	11.0	11.0–14.9	9.6–11.2	9.2–12.0
Interorbital width	7.6	5.4–6.0	6.3–8.2	6.5–7.8
Body depth	26.0	23.7–29.6	24.1–26.8	23.0–26.9
Depth of caudal peduncle	6.4	5.7–6.6	5.7–6.8	5.9–6.4
Length of caudal pecuncle	15.2	12.4–17.2	13.0–16.3	12.8–16.1
Predorsal length	37.7	39.6–44.2	34.2–38.1	35.2–37.4
Length of first dorsal base	20.8	17.7–23.1	18.8–22.9	18.4–22.6
Length of second dorsal base	31.6	25.4–30.6	30.6–35.4	29.5–33.9
Length of anal base	35.4	30.3–32.2	30.1–35.8	31.9–35.7
Length of longest dorsal spine	18.8	16.7–20.5	15.4–20.4	17.1–19.5
Length of longest pectoral ray	31.5	28.6–32.6	28.5–34.7	27.5–34.5
Length of pelvic fin	30.3	29.7–32.3	27.4–30.6	26.7–29.6
Depth of head	26.1	26.4–30.6	24.0–26.4	23.1–26.3
Head width	20.6	18.6–22.3	16.3–20.9	17.6–22.2
Snout length	14.4	13.6–14.4	11.8–15.4	12.9–15.3
Postorbital length of head	10.8	12.6–14.6	10.3–12.5	10.2–12.1
Suborbital width	9.7	8.1–10.5	8.7–9.7	8.4–10.2
Height of cheek	12.0	12.4–14.0	11.6–13.3	10.5–12.3
Length of eye	10.5	9.9–12.8	9.3–12.1	9.1–12.3
Length of upper jaw	12.3	15.0–17.4	12.4–14.0	11.8–13.0
Length of cleithral spine	11.0	9.9–11.7	9.6–11.9	9.5–12.2


Trigla gurnardus.
British Museum (Natural History)
A
53.11.12.15
British Museum (Natural History)
53.11.12.16
B
Trigla hirundo.
C
D

A. Holotype of *Chelidonichthys gurnardus* (Linnaeus) (BMNH 1853.11.12.:15):
B. Holotype of *Chelidonichthys lucernus* (Linnaeus) (BMNH 1853.11.12:16);
C. Neotype of *Chelidonichthys cuculus* (Linnaeus) (BMNH 1963.5.14:696);
D. Lectotype of *Lepidotrigla cadmani* Regan (BMNH 1914.11.2:51).

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A Research Aquarium Suitable for Shipboard Use

Efforts to keep juvenile pelagic fishes alive aboard Bureau of Commercial Fisheries research vessels, the *Geronimo* and the *Undaunted*, have been unsuccessful, for the last 3 years. The two major obstacles were: (1) pelagic fishes which are unaccustomed to contact with solid surfaces often injured themselves and died after they swam against, or struck, walls and corners of rectangular tanks; (2) even the usual rolling and pitching of vessels caused violent movement of water in rectangular aquaria, and in heavy seas aquarium lids were dislodged and water was spilled.

We eliminated these problems by constructing a circular aquarium with a permanent lid. The lid approximates the basic pattern of bait-tank lids used on commercial tuna clippers, and of portable holding tanks (Nakamura, 1966). It has a circular opening in the middle and a cylinder around the opening (Figure 1). This type of covering

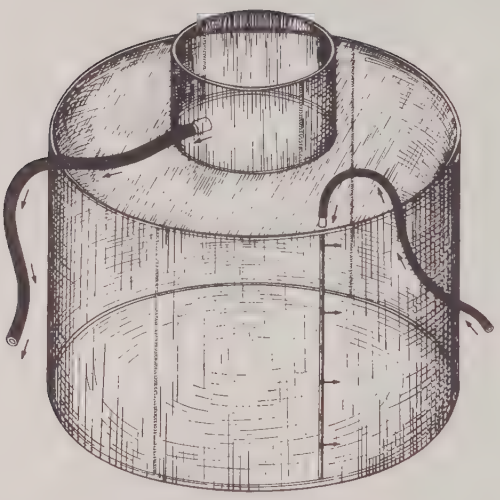

FIGURE 1.—A diagram of the aquarium. Arrows indicate direction of water flow in the intake and outflow lines. Vertical seams of the plexiglass are indicated by stippled lines.

reduces the swashing of aquarium water, when the water level is maintained at a level near the overflow pipe. The small open water area within the lid cylinder remains relatively stable even when the ship rolls as much as 30 degrees. The circular walls make it impossible for fish to trap themselves in corners; the efficiency of the circular construction is further increased by the introduction of a horizontal water current that orients the fish so that they seldom come in contact with the walls.

Three aquaria were constructed of clear ¼-inch thick plexiglass. The high cost of plexiglass was offset by the ease with which the material can be cut, bent, glued, and drilled. The aquaria were 30 inches in diameter and 18 inches high. The cylinder above the lid has a diameter of 12 inches and is 6 inches high. (Aquarium size was governed by the amount of space available on the R/V *Undaunted*.) The walls of each aquarium were constructed from two curved pieces of plexiglass as this is easier than bending one sheet into a full circle. The lid cylinder was similarly formed. Ethylene dichloride insured adherence of surfaces and water tightness. The total cost, including labor, for the three aquaria was about $500.00. A water (⅜-inch inside diameter) intake line was placed in a vertical position along the inside of the aquarium wall. Small 3⁄16-inch holes were drilled in the intake line along its entire length to create an even horizontal flow of water from the floor to the top of the aquarium. A drain (1-inch inside diameter) was placed 4 inches below the upper edge of the lid cylinder.

Two minor disadvantages have been encountered: (1) because plexiglass is soft and scratches easily, the appearance of the tank becomes marred; (2) the right angles between the small cylinder and the lid and between the lid and the walls permitted the fish to escape capture by dip nets, when the aquarium is full of water. The latter is easily overcome by lowering the water level.

Juvenile fishes (10 to 80 mm standard length) that have been successfully maintained for as many as 40 days at sea include: flying fish (*Cypselurus* spp. and *Parexocoetus brachypterus*), halfbeaks (*Hemiramphus* spp.), squirrelfish (*Holocentrus* spp.), carangids (*Caranx ruber, Naucrates ductor, Decaptrus* spp.), scombrids (*Euthynnus alletteratus*), nomeids (*Nomeus gronowi*), and sargassum fish (*Histrio histrio*). Contribution No. 64 from the U.S. Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Fla. 33149.

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WILLIAM J. RICHARDS
BARBARA J. PALKO
EDWIN L. SCOTT

U. S. Bureau of Commercial Fisheries
Tropical Atlantic Biological Laboratory
75 Virginia Beach Drive
Miami, Fla. 33149

A PENAEID POSTLARVAL CHARACTER OF TAXONOMIC VALUE[1]

ROBERT D. RINGO[2] AND GILBERT ZAMORA, JR.
Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas

ABSTRACT

The presence of spines on the dorsal carina of the sixth abdominal segment distinguishes postlarval brown shrimp (*Penaeus aztecus*) and pink shrimp (*P. duorarum*) from postlarval white shrimp (*P. setiferus*), which lack these spines. The spine character was validated by examination of postlarvae of known parentage—51 brown, 53 pink, and 99 white shrimp, 5 to 25 mm long.

INTRODUCTION

Studies of the biology of postlarval brown (*Penaeus aztecus*), pink (*P. duorarum*), and white (*P. setiferus*) shrimp have been hampered by difficulties in identifying them. Pearson's (1939) descriptions and Williams' (1959) provisional key have been used to identify postlarval brown and white shrimp of 10 mm in total length or less. Problems in identification of postlarvae 10 to 25 mm long were noted by Baxter & Renfro (1966) who mainly resorted to seasonal occurrence and size to distinguish postlarval brown and white shrimp entering Galveston Bay. Brown and pink shrimp are easily distinguished from white shrimp by the presence or absence of the rostral groove when the shrimp are above 25 mm long.

In examining postlarvae from Galveston Bay, we noted a morphologic character by which it is possible to distinguish brown from white shrimp when the individuals are between 10 and 25 mm in total length. The presence of spines on the dorsal carina of the sixth abdominal segment of brown shrimp and the absence of spines on the dorsal carina of white shrimp distinguish the two species. Spines, or their absence, are little needed for specific identification in larger shrimp because the rostral groove then present on brown shrimp distinguishes them from the nongrooved white shrimp. This character is especially valuable in areas such as the Galveston Bay system where pink shrimp are rarely found.

The objectives of this study were: (1) to validate the dorsal-carina character from known-parentage brown, pink, and white postlarval shrimp; (2) to determine the accuracy of Pearson's (1939) and Williams' (1959) characters in identifying known-parentage postlarvae; and (3) to determine whether the dorsal-carina character can be used to distinguish brown from pink postlarval shrimp.

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[1] Contribution No. 230, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.
[2] Present address: Bureau of Sport Fisheries and Wildlife, Division of River Basin Studies, Sacramento, California.

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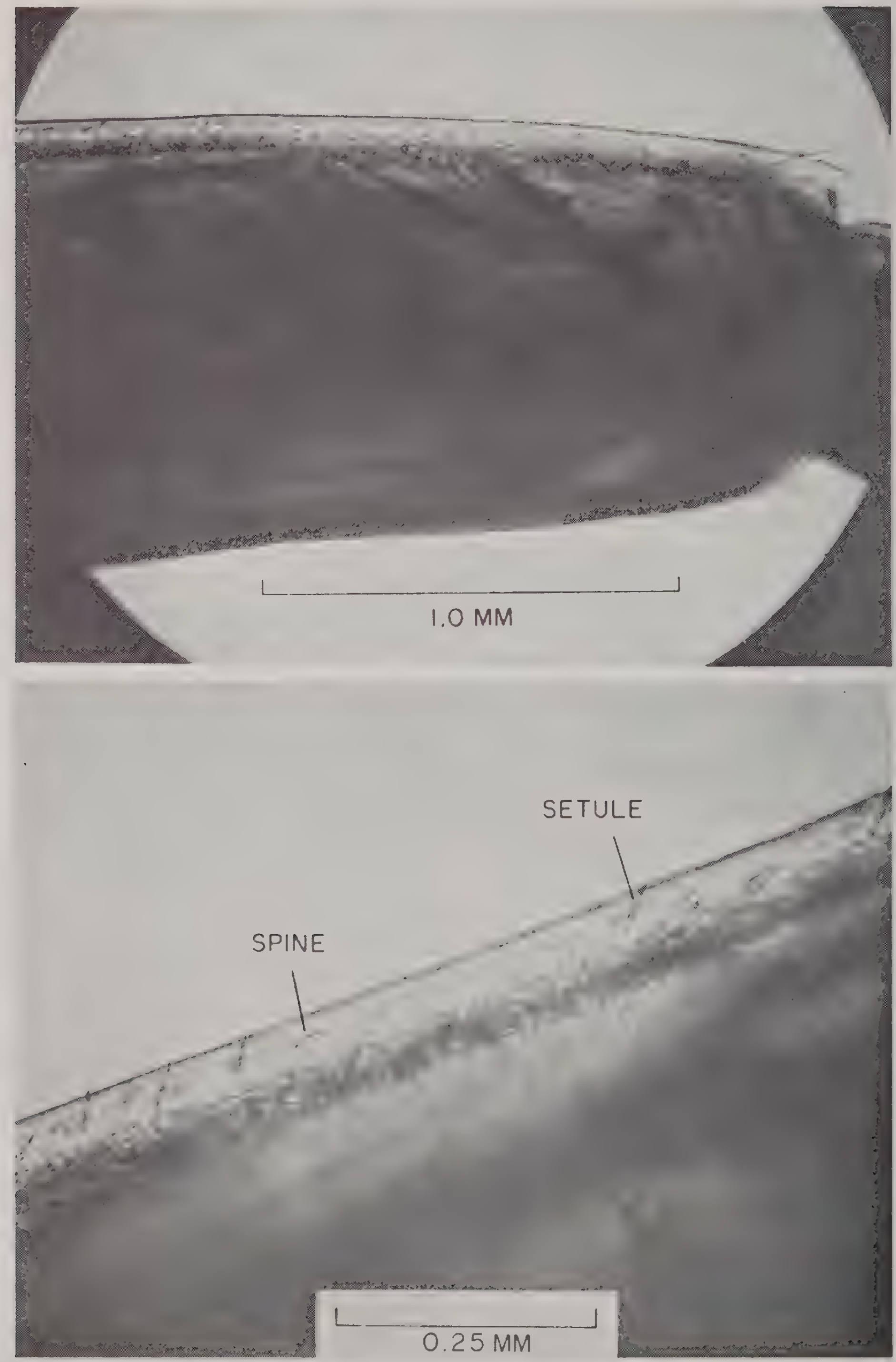
1.0 MM
SETULE
SPINE
0.25 MM

FIGURE 1. Dorsal carina spines on postlarval brown shrimp. Photographs of 13-mm postlarva at 19× (top) and 63× (bottom).

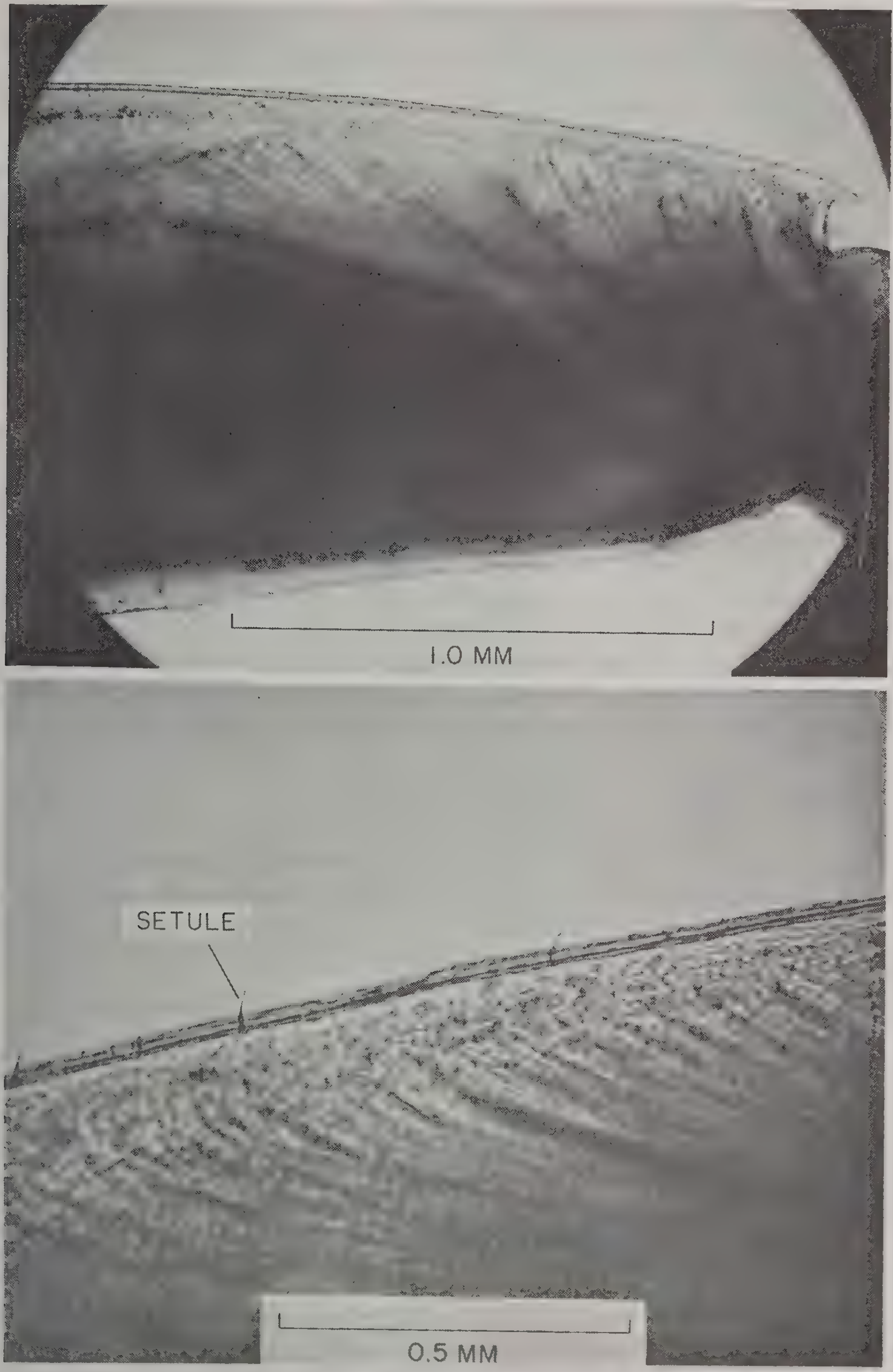

FIGURE 2. Dorsal carina of white shrimp, showing absence of spines. Photographs of 13-mm postlarva at 19× (top) and 63× (bottom).

Dorsal Carina Spines as a Character for Identification of Postlarval Shrimp

In this study, 51 brown, 53 pink, and 99 white postlarval shrimp of known parentage were examined. The shrimp were reared by Harry L. Cook and M. Alice Murphy, Bureau of Commercial Fisheries, Galveston, Texas.

Postlarvae were examined and measured at magnifications from 7× to 150×. Shrimp were measured to the nearest millimeter of total length (from tip of rostrum to tip of telson), and the occurrence and number of spines were recorded. Measurements of spines were made to the nearest 0.01 mm with a calibrated ocular micrometer.

On postlarval brown and pink shrimp 5 to 12 mm long, spines are in a discontinuous row on each side of the dorsal midline (precursor of the dorsal carina) of the sixth abdominal segment. At a length of 13 mm or more, the spines are usually in a continuous row on both sides of the dorsal carina (Fig. 1, top). Under low magnification (19×), the spines cause the dorsal carina to appear serrated. These same spines under higher magnification (63×) exhibit a robust appearance, having a broad base and short length that distinguish them from the setules (Fig. 1, bottom). The size of the spines increases with increase in the length of the shrimp. Spines were 0.01 mm or less in length on 5-mm postlarvae, but ranged from 0.02 to 0.04 mm on 13-mm postlarvae.

The absence of dorsal-carina spines on white shrimp (Fig. 2) clearly distinguishes postlarvae of this species from those of brown and pink shrimp.

To examine further the usefulness of the dorsal-carina spines in identification, all known-parentage brown and white shrimp were separated by using (1) the spine character, and (2) a combination of the following characters presented by Pearson (1939) and Williams (1959):

Brown shrimp	White shrimp
1. Rostrum extending to distal edge of eye.	1. Rostrum not extending to distal edge of eye.
2. Third pereiopod extending beyond distal edge of eye.	2. Third pereiopod not extending beyond distal edge of eye.
3. Posterior rostral spines far apart.	3. Posterior rostral spines close together.
4. Ventral rostral spines relatively near together and proximal.	4. Ventral rostral spines relatively far apart and distal.
5. Antennal scale broadly rounded.	5. Antennal scale acutely rounded.

We were 100 per cent accurate in separating postlarvae of brown and white shrimp using the spine character (Table 1). Errors ranged from 0 to 38 per cent when the same shrimp were separated with the characters given by Pearson (1939) and Williams (1959).

TABLE 1

Percentage Error in Identification of Known-parentage Postlarval Brown and White Shrimp in Relation to Length

Total length (mm)	Brown shrimp			White shrimp		
	Number examined	Number correctly identified	Percentage error	Number examined	Number correctly identified	Percentage error
			Spine character			
5– 6	11	11	0	7	7	0
7–10	14	14	0	21	21	0
11–25	26	26	0	71	71	0
			Pearson-Williams characters			
5– 6	11	7	36	7	7	0
7–10	14	14	0	21	20	5
11–25	26	16	38	71	48	32

The numbers of dorsal carina spines on known-parentage brown and pink shrimp (Table 2) demonstrate that the character cannot be used to separate postlarvae of these species. The number of spines for each species generally increases with increasing size. For shrimp of a given length, the number of spines differs little between the two species.

Acknowledgments

The authors express their apprecation to Mr. Harry L. Cook for technical laboratory guidance, Mr. Daniel Patlan for the photographs, and Mr. Lee Trent for valuable criticism of the manuscript.

TABLE 2

Average Number of Spines on Known-parentage Postlarval Brown and Pink Shrimp in Relation to Length

Total length (mm)	Brown shrimp			Pink shrimp		
	Number of specimens	Number of spines		Number of specimens	Number of spines	
		Average	Range		Average	Range
5– 7	12	2.2	1– 9	9	2.4	1– 8
8–10	13	12.5	4– 32	10	15.9	3– 34
11–13	5	30.6	20– 46	6	31.7	25– 40
14–16	3	59.0	52– 72	9	50.8	40– 59
17–19	6	76.8	55–104	2	59.0	58– 60
20–22	10	73.2	58– 90	4	71.5	68– 76
23–25	2	83.0	76– 90	13	75.3	46–100

SUMARIO

UN CARACTER DE VALOR TAXONOMICO EN LA POSTLARVA DE LOS *Penaeus*

La presencia de espinas en la carina dorsal del sexto segmento abdominal sirve para distinguir la postlarva del camarón carmelita (*Penaeus aztecus*) y del camarón rosado (*P. duorarum*) de la postlarva del camarón blanco (*P. setiferus*), que no tiene estas espinas. El valor de la espina como carácter distintivo fue establecido tras el examen de postlarvas de origen conocido—51 carmelitas, 53 rosadas y 99 blancas, de 5 a 25 mm de longitud.

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HERMAPHRODITISM IN THE SURF CLAM, *SPISULA SOLIDISSIMA*

John W. Ropes
U. S. BUREAU OF COMMERCIAL FISHERIES
BIOLOGICAL LABORATORY
OXFORD, MARYLAND

ABSTRACT

A single hermaphroditic surf clam, Spisula solidissima *(Dillwyn), was found among 2,500 clams collected to determine the seasonal reproductive cycle in the mid-Atlantic bight. Standard histological techniques were used to prepare stained sections of all gonads for detailed microscopic examination. The hermaphroditic specimen contained clearly distinguishable testicular and ovarian alveoli with developing germ cells of both sexes. The rarity of hermaphroditism in the surf clam is discussed in relation to this condition in other pelecypods.*

Hermaphroditism has not been reported for the the surf clam, *Spisula solidissima* (Dillwyn), a pelecypod that normally is dioecious (Belding, 1910). The simultaneous production of male and female germ cells within an individual is common in many gastropods, but is relatively rare in pelecypods (Coe, 1943, 1944; Galtsoff, 1961).

A hermaphroditic surf clam was collected on June 19, 1965, in an experimental jet dredge (Merrill and Webster, 1964) towed at a site 34 miles (ca. 63 km) east of False Cape, North Carolina (75° 10′ W. Long., 36° 38′ N. Lat.). Water depths ranged from 90 to 105 feet (ca. 27 to 32 m). This drag was one of many made during a study underway since 1962 to determine the seasonal reproductive cycle of surf clams. Eleven clams averaging 142 mm in shell length were taken in the 5-minute tow. The gonads were preserved in Bouin's fixative, and standard histological techniques were used to prepare 7 μ-thick sections for microscopic examination.

The hermaphroditic condition was not detectable in the freshly opened clam. Color differences between gonads of male and female surf clams are not obvious, but in the slide preparation a difference in stain intensity is apparent between the male and female alveoli (Fig. 1A). The darkly stained portions of the gonad contain male germ cells; the lightly stained portions contain female germ cells. The specimen is an example of bilateral hermaphroditism (Coe and Turner, 1938).

Both active gametogenic and ripe developmental phases are present in the testicular alveoli of the hermaphroditic clam. The tubelike alveoli are closely packed in the cross-sectioned gonad; interalveolar cells are sparse between the basement membranes of connective tissue. As is typical of active gametogenesis, primordial germ cells form a layer of several cells in one area of the gonad (Figs. 1B & 1C). Spermatogonia, and primary and secondary spermatocytes occur respectively from the basement membrane toward the lumina of alveoli, and spermatids and sperm are in the centers. In comparison with the ripe phase, however, the alveoli contain few germ cells, and especially sperm. Typical of the ripe developmental phase, sperm form a dense mass in the lumina of alveoli in another area of the gonad (Fig. 1D). Primordial germ cells lie nearest the basement membrane, and are less numerous than sperm.

The ovarian alveoli contain early developing ovocytes, typical of active gametogenesis, although a few ripe ovocytes are present in the lumina (Figs. 1B, 1C, & 1D). Early ovocytes protrude from the basement membrane, advanced ovocytes are attached by stalks, and ripe ovocytes lie free within the lumina and contain amphinucleoli (Allen, 1953).

Variability in development throughout a gonad is common; it was observed by Coe (1932) in the California oyster, *Ostrea lurida*, a species that undergoes a sex reversal and also has true hermaphroditic individuals in its populations. Coe (1943) hypothesized that in ambisexual oysters the sex-differentiating mechanism apparently fails to function normally. A tendency for sperm to ma-

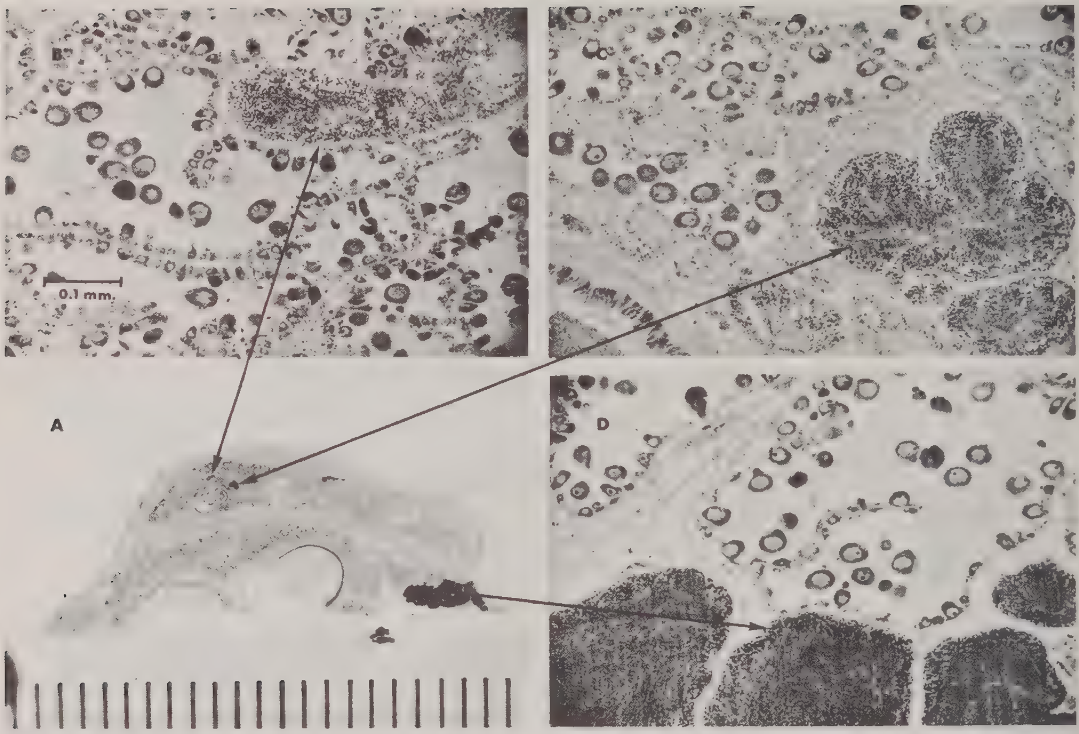

FIG. 1 *Sections of the gonad of a hermaphroditic surf clam,* Spisula solidissima. *(A) a macroscopic view of the section showing three areas of testicular alveoli stained more intensely than the adjacent ovarian alveoli. A millimeter scale is included in this photograph and arrows point to microscopic enlargements (100X) of areas containing testicular alveoli. (B & C) Two areas of testicular alveoli containing mostly primordial germ cells and primary and secondary spermatocytes. (D) Another area of testicular alveoli containing dense masses of mature sperm. Ovarian alveoli are adjacent to the testicular alveoli in all of the enlargements and contain developing ovocytes.*

ture in advance of ova in one area of the surf clam gonad (Fig. 1D), but at the same rate as ova in other alveoli (Figs. 1B & 1C) is perhaps a deviation from the normal developmental process.

Typically dioecious pelecypods produce few hermaphrodites. Coe and Turner (1938) found only three hermaphroditic soft-shell clams, *Mya arenaria,* in about a thousand obtained near New Haven, Connecticut. Shaw (1965) found no hermaphrodites in 800 soft-shell clams from Chesapeake Bay, Maryland, and Ropes and Stickney (1965) found no hermaphrodites in 1,400 *Mya* collected from nine areas along the New England coast. Loosanoff (1936) reported only two hermaphrodites in several hundred quahogs, *Mercenaria mercenaria.* The discovery of first one and then another hermaphroditic sea scallop, *Placopecten magellanicus,* by Merrill and Burch (1960) was interrupted by an inspection of about 3,000 normal gonads. The single hermaphroditic surf clam in a sample of nearly 2,500 must be an anomaly and would, then, be termed an "accidental functional ambisexual" by the classification of Coe (1943).

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REPRODUCTIVE CYCLE OF THE SURF CLAM, SPISULA SOLIDISSIMA, IN OFFSHORE NEW JERSEY

JOHN W. ROPES

U. S. Bureau of Commercial Fisheries, Biological Laboratory, Oxford, Maryland 21654

Atlantic surf clams, *Spisula solidissima* (Dillwyn), were collected from offshore New Jersey during a three and one-half-year period to obtain their gonads for histological treatment in a study of the annual reproductive cycle. Documentation of the annual reproductive cycle on the basis of gonad distention (Westman and Bidwell)[1] and excision of gametes (Allen, 1951, 1953; Schechter, 1941) is incomplete and fragmentary. Neither gonad distention nor excision of gametes assesses the events of gamete development within the gonad. Also, parasites are a possible source of error if the technique of observing gonad distention is used. I have seen infected surf clams with distended gonads when those of uninfected individuals were shrunken. Gonad color has been used as an indicator of sex and gonad development of the sea scallop, *Placopecten magellanicus* (Posgay and Norman, 1958; Merrill and Burch, 1960). The color of surf clam gonads containing mature sex products, however, is not consistent. Ovaries of females are sometimes pink, but may also be white, as are the testes (Schechter, 1941).

Periodic histological examinations of gonad tissue during several successive years has been a valuable method of determining the annual frequency and duration of the reproductive cycle in many marine invertebrates (Giese, 1959). The reproductive cycles of the soft-shelled clam, *Mya arenaria* (Pfitzenmeyer, 1962, 1965; Shaw, 1962, 1965; Ropes and Stickney, 1965) have been recently established by describing the cytological events within the gonad. Such events within the gonads of surf clams from an area of intensive fishing off the New Jersey coast have been related to water temperature. The present study of seasonal gonad development was undertaken to determine the annual frequency and duration of spawning—information basic to understanding larval occurrence and time of setting of juvenile surf clams.

Materials and Methods

Surf clam gonads were collected from port landings (1962 and 1963) and commercial and research vessels (1964 and 1965). In all years, samples were taken as soon as practicable after the clams were removed from the water, because the surf clam readily reacts to artificial spawning stimuli (Stickney, 1963) and some released sex products soon after capture. All samples were from the vicinity of Barnegat Lightship and were caught by hydaulic dredges operating at depths of 18 to 32 meters. A sample was taken monthly during the winter and biweekly during the spring, summer, and fall. Each sample comprised 25 live clams with shells 120 mm. long or longer. The portion of the gonad ventrad to the heart was removed after fixation of the entire visceral mass in Bouin's solution, thereby preventing the loss of eggs and sperm, and minimizing the possible variability in development within a single gonad. Standard histological techniques were employed to prepare sections 7 μ thick for staining with Delafield's hematoxylin and eosin.

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[1] Westman, J. R., and M. H. Bidwell, 1946. The surf clam. Economics and biology of a New York marine resource. State of New York Conservation Dept. Unpublished manuscript on file at Bureau of Commercial Fisheries Biological Laboratory, Oxford, Maryland 21654.

After microscopic examination of the section, each specimen was assigned to a category of gonad development. The proportions of clams in each category, regardless of sex, were recorded for individual samples and the samples were combined each month to simplify presentation. In graphic presentations of the results, the combined data are plotted at a date midway between the sample dates.

The possible influence of temperature on gonad development and spawning was considered. Surface and bottom sea-water temperatures at Barnegat Lightship were obtained from Chase (1965, 1966) for 1962 and 1963 and from unpublished records for 1964 and 1965.

Anatomy and Spawning

Male and female surf clams are distinguishable by microscopic examination of the gonads because they are unisexual or dioecious (Coe, 1943). Hermaphroditism is rare and then is apparently a developmental accident (Ropes, 1966).

The gross features of a surf clam's reproductive anatomy include anastomosing gonadal alveoli which lie ventrad to the pericardial chamber and overlay the dark brown digestive gland or liver mass, and surround the coiled intestine. In the distended gonads before spawning, the root-like alveoli are crowded close to each other and are filled with "late ripening" and "ripe" sex cells; their connective tissue walls are stretched thin; and they occupy much of the visceral mass. After spawning the alveoli contract, their walls thicken, and mesenchyme is interspersed between them; the dark brown digestive gland is then the most prominent organ and the visceral mass is flaccid.

The alveoli lead into a pair of gonoducts, each of which has an enlarged portion that serves as a reservoir for ripe sex cells before spawning (Stickney, 1963). The gonoducts terminate at the genital apertures on minute papillae that protrude from the surface of the posterior foot retractor muscle on each side of the visceral mass.

The passage of water for respiration and digestion conducts sex cells from the clam into the surrounding water during spawning. Water drawn through the incurrent siphon flows into the infrabranchial chamber, around the gills, past the genital papillae, into the epibranchial chamber, and then out through the excurrent siphon. Spawning is often accompanied by rhythmic contractions of the adductor muscles which pull the two valves together. Gametes are either emitted into the water by the muscular activities or flow out. Ovocyte maturation follows spawning and fertilization (Costello *et al.*, 1957; Stickney, 1963) but meiosis occurs in the gonads of male surf clams and functional sperm are developed before spawning.

CATEGORIES OF GONAD CONDITION

In this study the more or less continuous reproductive process was divided into five phases as described below. The demarcation between phases is not sharp—the divisions are convenient rather than natural.

Female gonads

1. *Early active phase*

In the early active phase ovogonia appear at the periphery and are embedded in the alveolar walls, often before the gonads are completely empty of ripe ovocytes. The round and oval nuclei of ovogonia contain distinctly basophilic nucleoli and the nucleoplasm has thin, irregularly shaped, dark-staining threads (Fig. 1). Cytoplasm surrounds the nuclei but is indistinct and of irregular shape. The ovogonia are possibly undergoing the pre-meiotic stages similar to those described for the desert snail, *Eremina desertorum* (Fahmy, 1949) and the soft-shelled clam, *Mya arenaria* (Coe and Turner, 1938). The alveolar walls are not completely contracted and lumina are evident in most gonads.

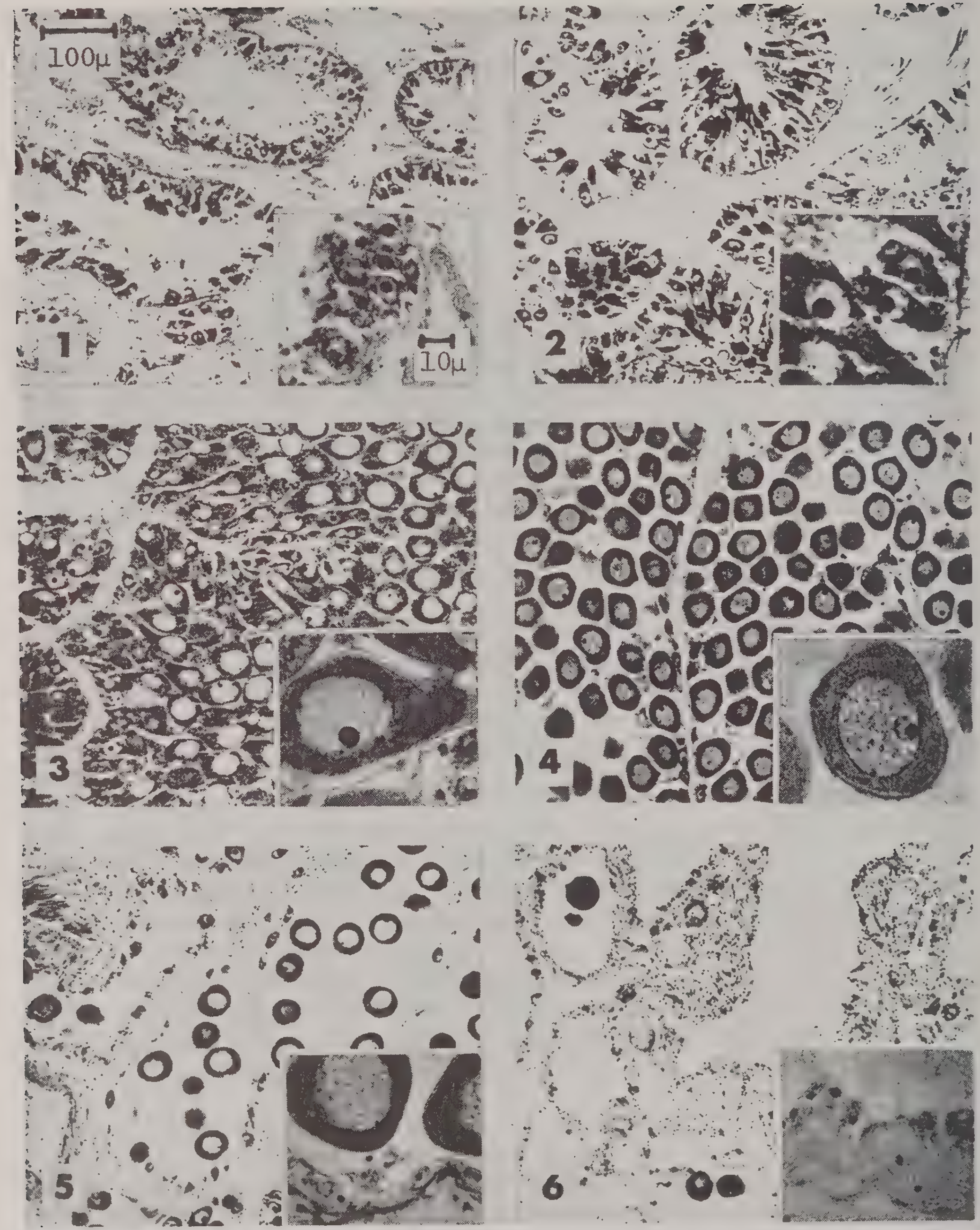
The early ovocytes also have mostly round and oval nuceli containing basophilic nucleoli, but the nucleoplasm is homogeneous and almost clear (Fig. 2). The ovocytes lie at the periphery of the alveolar walls and the cytosome extends into the lumen of the alveolus, where a rounded cap is formed. The shape of the ovocytes may be square, triangular, cylindrical, or hemispherical. All of these ovocytes are attached to the basement membrane by a stalk. The diameters of the nuclei range from 5 to 20 μ and average 11.1 μ.

2. *Late active phase*

Ovocytes in the late active phase are larger than early ovocytes and many are round (Fig. 3). The nuclei contain basophilic nucleoli and the nucleoplasm is homogeneously granular. The nuclei, surrounded by cytoplasm, are the most conspicuous characteristic of the cells. Some ovocytes are attached to the basement membrane of the alveoli by a thin stalk, but most are free in the lumina. The basement membrane is thin—apparently due to the increased volume of cells within the alveoli. The diameters of the nuclei range from 14 to 32 μ and average 24.1 μ.

3. *Ripe phase*

In ripe clams, ovocytes are free in the lumina of the alveoli. The vitelline membrane contains the cytoplasm and a large nucleus (Fig. 4). These ovocytes are very similar to those in the late active phase except for the presence of prominent amphinucleoli (Allen, 1953). Each amphinucleolus consists of an almost transparent, granular nucleolus and a small opaque, basophilic nucleolinus. Ripe gonads typically have a dense appearance because the alveoli are crowded together and are filled with large ovocytes. The diameters of the nuclei range from 22 to 33 μ and average 28.5 μ.



FIGURES 1–6.

FIGURE 1. Section of gonad tissue from a female surf clam, early active phase of the first annual reproductive cycle. All of the large photomicrographs are reproduced at the same magnification and a scale (100 μ) is provided. The small photomicrographs inserted in the lower right-hand corner of each figure are enlargements of portions of the gonad all at the same magnification and a scale (10 μ) is provided. Collection date: 21 January 1964.

4. *Partially spawned*

A few large, ripe ovocytes are free in the lumina of some alveoli of partially spawned clams; other alveoli are completely void of ripe ovocytes (Fig. 5). Ovogonia and early ovocytes appear in the contracted and thickened alveolar walls. The spaces between alveoli contain mesenchyme and the whole gonad has a loose, flaccid appearance. In some clams, ripe ovocytes are being cytolyzed.

5. *Spent*

In typical spent clams, the open lumina of alveoli are usually void of ripe ovocytes. The thickened alveolar walls contain ovogonia and early ovocytes (Fig. 6). Mesenchyme occurs in the spaces between the loosely arranged alveoli.

Male gonads

The criteria for the five categories of gonad condition in the male are presented below:

1. *Early active phase*

Clams in the early active phase contain cells undergoing the initial meiotic stages of development. Darkly stained spermatogonia are in the thickened alveolar walls (Fig. 7). Primary spermatocytes about 3 to 4 μ in diameter proliferate toward the lumina from a close contact with the alveolar walls and form single cell columns (Fig. 8). Their large, round and oval nuclei are surrounded by thin irregularly shaped cytoplasm. Two basophilic nucleoli within some cells indicate that cell division is taking place. The nucleoli are less basophilic and smaller than those in the earliest ovocytes.

2. *Late active phase*

The remaining spermatogenic stages are seen in clams in the late active phase. Secondary spermatocytes of about 2 to 3 μ in diameter with dark basophilic chromatin threads that nearly fill the nuclei are numerous and the surrounding cytoplasm is irregular in shape and very indistinct (Fig. 9). Small and strongly basophilic spermatids measuring about 1.5 μ in diameter form dense masses near the centers of the alveoli. A transformation of the spermatids results in the appearance of sperm in the lumina. The sperm form weak columns with the tails oriented toward the centers of alveoli. The sperm heads are about 1 μ in diameter.

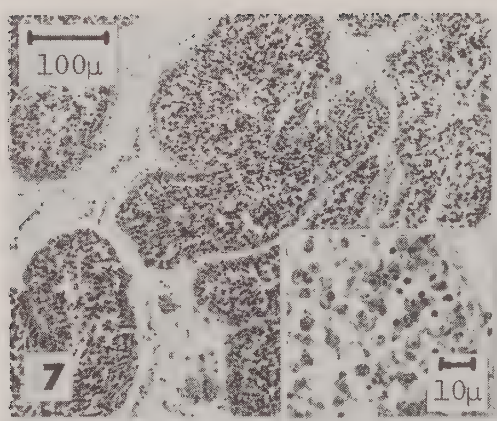
FIGURE 2. Same from a female surf clam, early active phase, showing enlarging ovocytes. Collection date: 18 February 1964.

FIGURE 3. Same, from a female surf clam, late active phase, showing large oval ovocytes. Collection date: 18 February 1964.

FIGURE 4. Same, from a female surf clam, ripe phase. Collection date: 26 June 1964.

FIGURE 5. Same, from a female surf clam, partially spent phase. Collection date: 28 August 1964.

FIGURE 6. Same, from a female surf clam, spent phase. Collection date: 13 August 1964.



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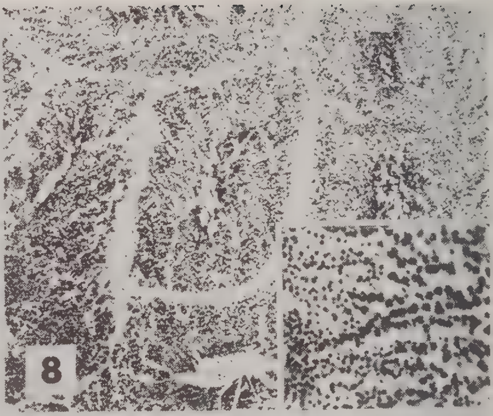

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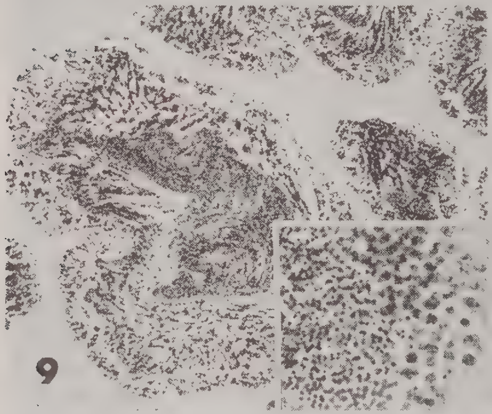

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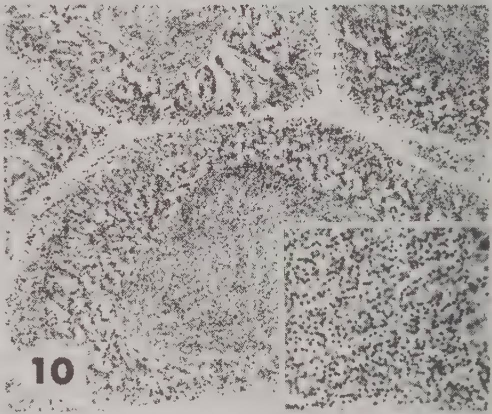

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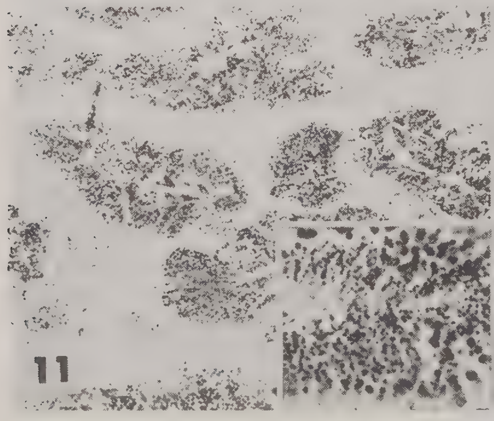

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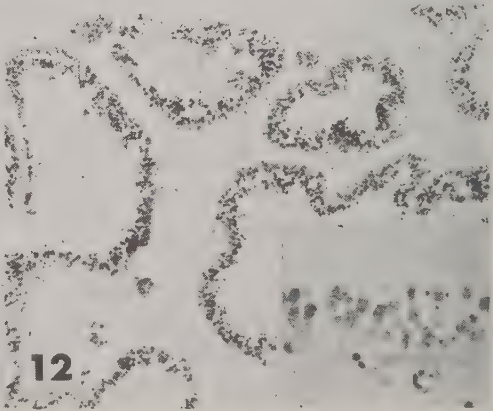

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FIGURES 7–12.

FIGURE 7. Section of gonad tissue from a male surf clam, early active phase of the first annual reproductive cycle. Collection date: 21 January 1964.

FIGURE 8. Same, from a male surf clam, early active phase, spermatozoa form columns. Collection date: 18 February 1964.

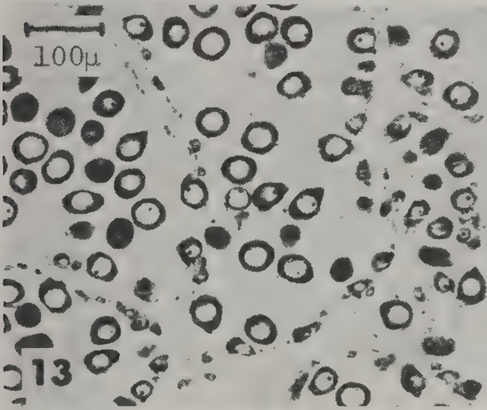
FIGURE 9. Same, from a male surf clam, late active phase. Collection date: 3 June 1964.

3. *Ripe phase*

Mature sperm form dense masses in the alveoli of clams in the ripe phase (Fig. 10). The sperm appear to be swirling in the centers of some alveoli, in others their tails are oriented toward the centers of alveoli, and in still others they form a homogeneous mass. Cells in early stages of spermatogenesis at the periphery of alveoli are much less numerous than the sperm.

4. *Partially spawned phase*

Partially spawned male clams still contain spermatozoa within the centers of alveoli, but they are substantially less numerous than in ripe clams (Fig. 11). The alveolar walls are compressed and thickened. Like the ovogonia and early ovocytes at this stage, spermatogonia and primary spermatocytes are developing along the basal membrane before most gonads are completely void of spermatozoa.



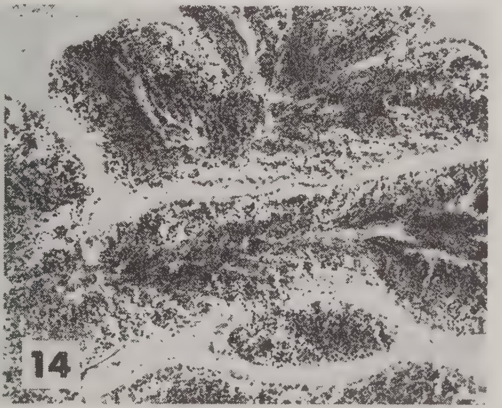


FIGURE 13. Section of gonad tissue from a female surf clam, ripe phase of the second annual reproductive cycle. Collection date: 24 September 1964.

FIGURE 14. Section of gonad tissue from a male surf clam, ripe phase of the second annual reproductive cycle. Collection date: 24 September 1964.

5. *Spent phase*

The alveoli of spent male clams contain no spermatozoa or very few and the lumina are characteristically open (Fig. 12). Primary spermatogonia are proliferating from the alveolar walls.

SECOND ANNUAL CYCLE

A second annual maturation of New Jersey surf clams was observed during three of the four years and was essentially a repetition of the sequence in gonad conditions already presented. The second maturation seemed to be of minor

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FIGURE 10. Same, from a male surf clam, ripe phase, a dense mass of spermatozoa is formed. Collection date: 15 July 1964.

FIGURE 11. Same, from a male surf clam, partially spawned phase. Collection date: 29 July 1964.

FIGURE 12. Same, from a male surf clam, spent phase. Collection date: 29 July 1964.

importance, however, since fewer ovocytes appeared in the gonadal alveoli (Fig. 13). Counts of the number of ovocytes in 1.25 mm.^{2} of gonadal tissue sections of ripe clams from the two reproductive cycles in 1964 showed an average density of 44.2 ovocytes for 32 ripe clams from the first cycle and 26.4 ovocytes for 20 ripe clams from the second cycle. The sperm in male gonadal tissues also appeared to be less numerous during the second cycle (Fig. 14).

Annual Reproductive Cycles in Relation to Water Temperature

An account of the gonad conditions in 1514 surf clams and bottom water temperatures taken in the area sampled for clams is presented in chronological order. Gonad collections were initiated in June, 1962, and continued through 1965; water temperature data were available for the period 1962–65. Unless otherwise specified, all references to water temperature are for the bottom.

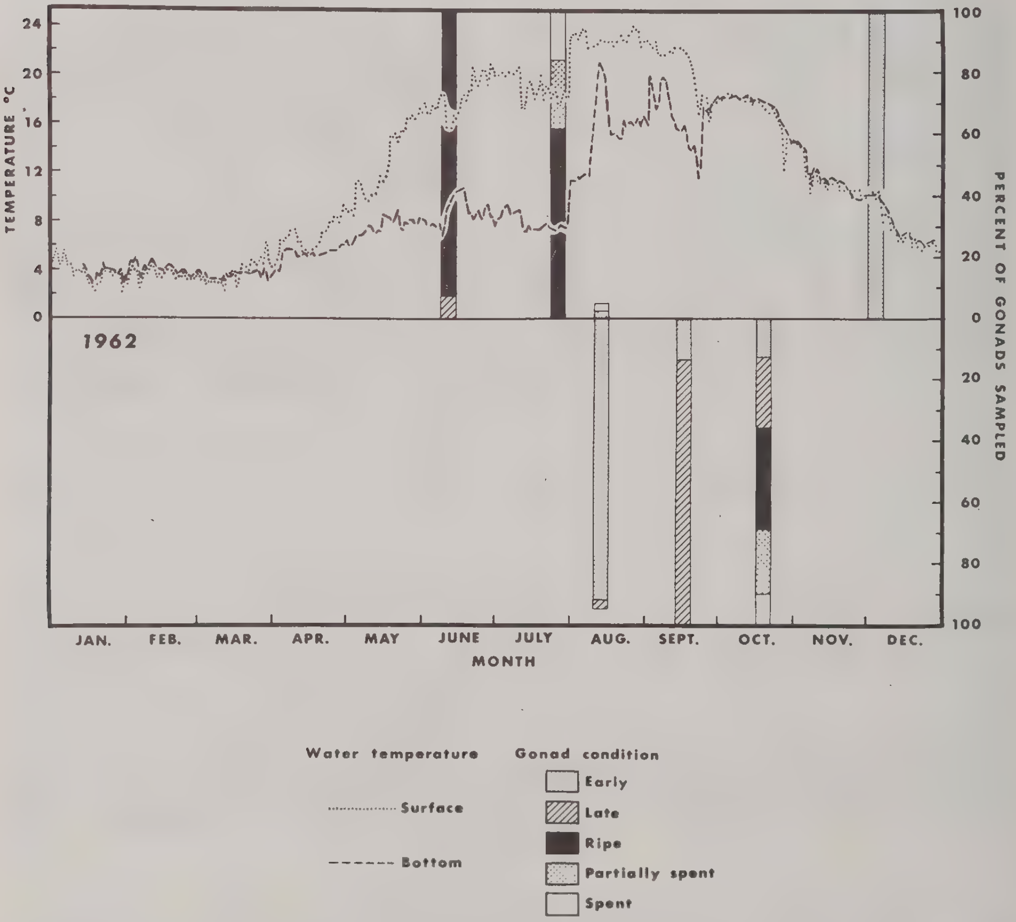

FIGURE 15. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1962. The bars above the centerline represent a single reproductive cycle and those below the centerline represent a subsequent cycle.

Reproductive cycle and water temperature in 1962

The June and July samples contained mostly ripe clams (Fig. 15). Spawning began by about mid-July when 37% of the clams were in the partially spawned and spent condition, and was completed by mid-August when 94% of the clams were in the early active phase. All clams were in the early and late active phases during September. All phases of gonad condition were represented in the October sample. A second spawning was apparent in mid-October when 32% of the clams were partially spawned and spent. All clams collected in early December were in the early active phase.

The temperatures were lowest (2.2° C.–5.2° C.) in late January, February, and early March. A warming trend followed, and 8° C. was reached by mid-May. The temperature reached 10.7° C. in mid-June, but most temperatures were between 7° C. and 9° C. during the 1½ months preceding the mid-July spawning. Spawning began 1 to 2 weeks before a rapid temperature rise, from 8° C. to 21° C., during late July to mid-August. Clams in the early active phase of a second reproductive cycle were most numerous when the temperature had reached its seasonal high (21° C.). The second spawning was in October, during a period when temperatures dropped from a high of 18° C. to about 10° C.

Reproductive cycle and water temperature in 1963

All of the clams were in the early active phase in January (Fig. 16). Gonads were in the late active phase in 4% of the clams by mid-February and in 56% of the clams by mid-March. Ripe clams constituted 92% of the mid-May sample and 98% of the mid-June sample. Spawning began in early July when 60% of the clams were partially spawned or spent. During August, 75% of the clams were still partially spawned or spent. The first annual spawning must have been completed by the end of August, because by mid-September 96% of the clams were in the late active and ripe phase. In mid-October collections, 28% of the clams were partially spawned and spent—evidence of a second spawning. Most (92%) of the clams were in the early active phase by early December.

Winter temperatures fell to a low of 2° C. during February. A warming trend after March (bottom temperatures are not available for March) was gradual and without marked fluctuations. The temperature on the bottom reached 10° C. by early June and 11° C. by late June. Temperatures reached 12° C. in mid-July. Spawning in July and August preceded a rapid rise in temperature from 9.6° C. to 18.9° C. during the early part of September. The beginning of a second reproductive cycle coincided with the rapid rise in temperature. The second spawning in October was during a period when temperatures dropped from 17° C. to about 15° C.

Reproductive cycle and water temperature in 1964

All clams were in the early active phase in January (Fig. 17); 63% were in the late active phase in February and this condition predominated in March and April. Gonads were ripe in 79% of the clams in May and in all of the clams in June. Spawning occurred in early July (43% of the clams were in the partially spawned and spent condition in mid-July). Fifty-three per cent of the clams were partially spawned and spent in mid-August and the rest were in the early active phase. A progressive development of the gonads during September and October was followed by a second spawning late in the year; 68% of the clams were partially spawned and spent in early November. In early December, 80% of the clams were in the early active phase.

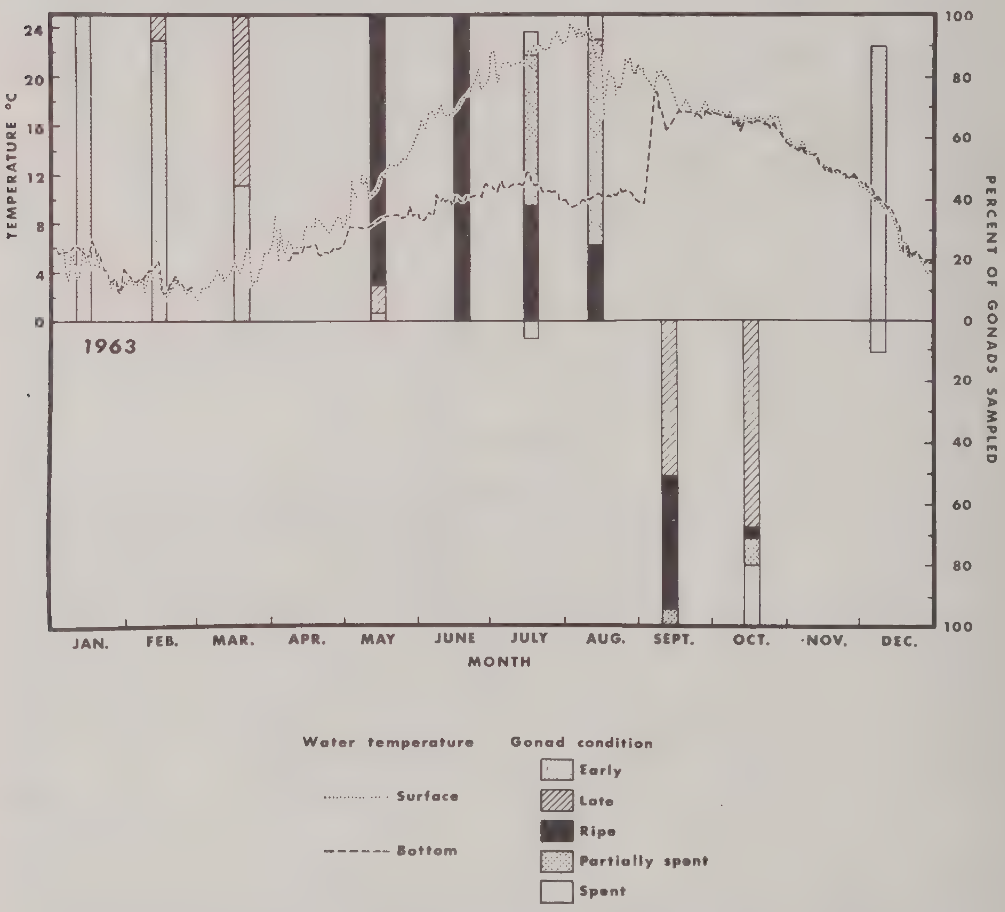

FIGURE 16. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1963.

The period of low winter temperature from January through March included a drop to 2° C. in February and was followed by a warming trend in April. In May and June the bottom temperatures fluctuated between 7° C. and 9° C. A temperature of 11° C. was reached in early July and was a possible inducement to spawning. All of the clams were completely spawned out in August after the rapid rise in temperature (7.4° C.–18.6° C.) during late July. The second reproductive cycle was underway in 47% of the clams after the rapid rise in temperature. The second spawning was during a period when temperature dropped from 16° C. to about 12° C.

Reproductive cycle and water temperature in 1965

All clams were in the early active phase during January and February (Fig. 18). The late active phase appeared in 76% and 62% of the clams during March and April, respectively. Ripe clams made up 94% of the late June sample and continued to predominate in the July, August, and September samples. In July and August only 7% to 11% of the clams were partially spawned and from mid-September to mid-October 29% to 52% of the clams were partially spawned or spent. Thus a mid-year spawning observed during the 3 previous years of the study was delayed 2 months in 1965. A few clams (7% to 13%) were in the spawning condition in late November and mid-December. From mid-October through December, however, many clams (48% to 93%) were in the early active phase. No second reproductive cycle was observed.

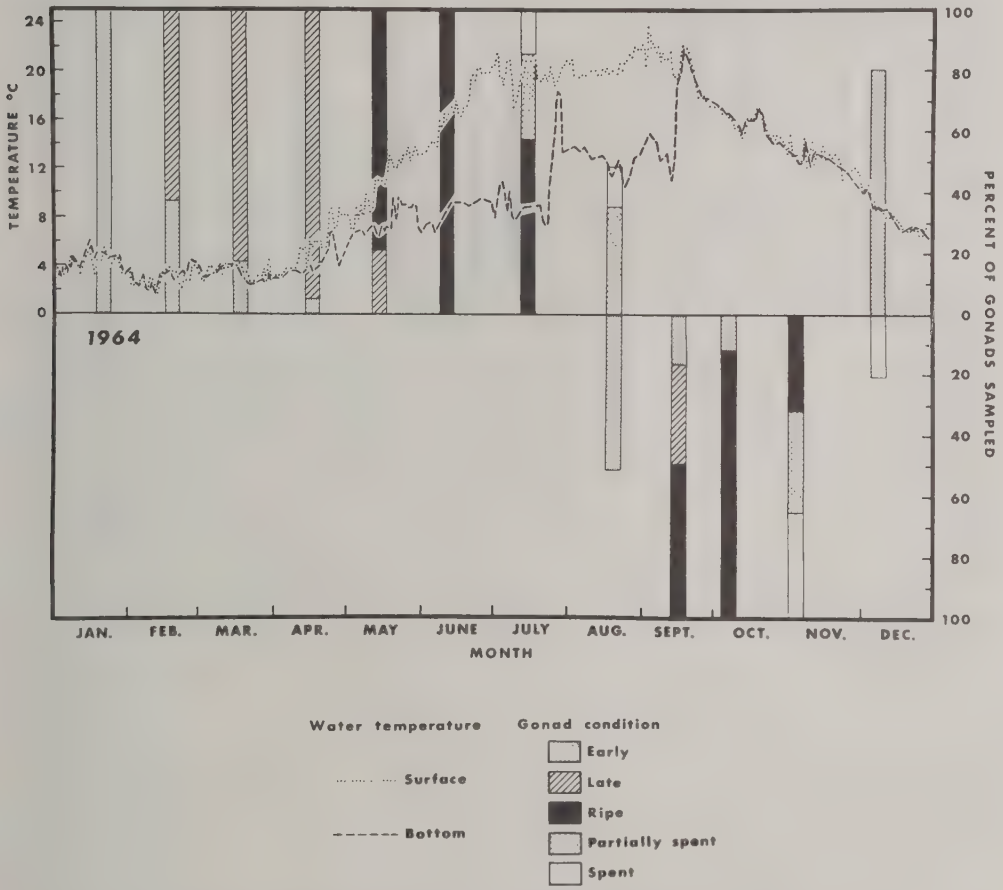

FIGURE 17. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1964.

Low winter temperatures were approximated from the surface observations because bottom temperatures were not available until early May. Warming to about 6° C. in May was followed by temperatures of about 8° C. in June and July; fluctuations of 2° C. occurred but the temperature did not exceed 10° C. Temperatures of 11° C. were recorded on three occasions in August. Temperature rose sharply from 10° C. to 18° C. in mid-September. Unlike the sequence in the 3 earlier years, spawning apparently occurred after the sharp rise in temperature.

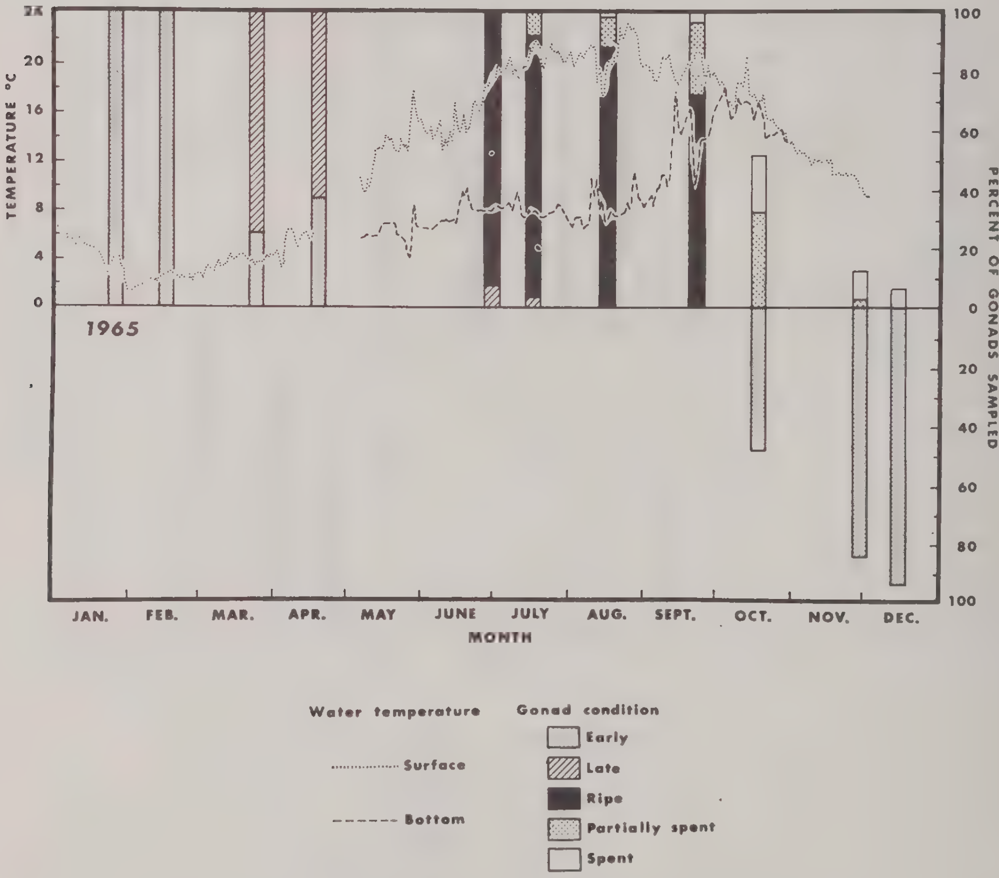

FIGURE 18. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1965.

DISCUSSION

In this study the term "reproductive cycle" includes the earliest detection of sex cells during periodic histological examinations of gonad tissue, the growth of female sex cells and multiplication of male sex cells which eventually fill the gonadal tubules, and the disappearance of sex cells from the tubules during the spawning period. The reproductive cycle can be separated into the gametogenic period (*i.e.*, the early, late, and ripe phases) and the spawning period (*i.e.*, partially spawned and spent phases). No period of inactivity was apparent in the sections of surf clam gonads, since sex cells for a succeeding reproductive cycle were detected in spent individuals (Figs. 6 and 12). In fact, separating the reproductive cycles of some marine invertebrates into an "inactive phase," "rest period," "quiescent period," or "vegetative phase" may only be a convenience (Ropes and Stickney, 1965). Biological processes maintaining life and early gametogenesis could very well be taking place during the inactive phase and be undetected by the histological technique used.

Examinations of the slide preparations of gonads provide an accurate basis for describing the reproductive cycle of surf clams from offshore New Jersey. Sex cell development began during December and, concurrent with the enlargement of the gonads, was followed by the occurrence of numerous partially spawned and spent clams during July and August each year from 1962 through 1964. A second maturation of sex cells followed the mid-year spawning, but gonad distention was minimal. Partially spawned and spent clams in the mid-October to early November samples in 1962 through 1964 was evidence of a second annual spawning. Although a biannual reproductive cycle may be typical for surf clams from offshore New Jersey during most years, a single reproductive cycle and spawning in 1965 was an important exception. The time and frequency of spawning each year, then, can vary.

Detection of a biannual reproductive cycle in surf clams from offshore New Jersey would be difficult without microscopic examinations of gonads throughout several calendar years. Westman and Bidwell (1946, see footnote 1) reported a mid-year spawning of surf clams from offshore Long Island, New York, by observing gonad distention and shrinking after spawning, but their method of visually determining gonad condition might not be precise enough to identify a second annual spawning, if one occurred. Allen (1951, 1953) observed a scarcity of eggs in surf clams from Woods Hole, Massachusetts, during 1 to 2 weeks in mid-summer coincident with a period of excessive heat. A possible explanation is that the clams had spawned or, since he continued to collect eggs for a 2- to 3-month period after mid-summer, these eggs may have been produced during a second annual reproductive cycle.

Temperature frequently influences the reproductive cycle and spawning of marine invertebrates (Giese, 1959; Loosanoff and Davis, 1963). During the gametogenic period, the surf clams in the beds off New Jersey were surrounded by gradually increasing, but fairly stable temperatures for the first six months in the three early years of the study. A progressive development of the gonads to a turgid and ripe state during the period of warming to temperatures of 12° C. or a little less preceded the first annual spawning. In 1965, however, the water temperatures during the gametogenic period were generally colder (8° C. or less) and more erratic (highs to 11° C.) than in the previous years. Gametogenesis was slightly delayed by the lower temperatures—94% of the clams were in the ripe phase by late June, 1965, whereas 100% were in the ripe phase by mid-June of 1962, 1963, and 1964.

Temperature was not clearly a stimulus to spawning of surf clams in their natural beds off New Jersey. Spawning by some clams did not accompany abrupt temperature changes in all 4 years, although more clams spawned before the abrupt temperature change in 1962–64 than in 1965. Spawning by some bivalves can be effectively delayed by holding them at low temperatures. Conversely, gonad development to a ripe condition has been hastened by holding bivalves in warm sea water.

The ripe bivalves have been spawned "out of season" and have produced normal larvae (Loosanoff and Davis, 1963).

I have held surf clams in 20° C. water from late February to mid-April, 1967 and compared their gonadal development with that of clams from the parent population in Chincoteague Inlet, Virginia. Gonads of all clams in the inlet were in the late active phase in late February and remained in this condition until after April. Water temperatures during the experimental period gradually increased from 5° C. to 11° C. In contrast, 10 gonads from clams held in the warmed water were all in the ripe phase by mid-March. On 11 April, a female spawned spontaneously in one of the containers and 2 partially spawned individuals were found when gonad sections of 10 clams were examined. These three specimens, then, spawned without the stimulus of a thermal shock and were perhaps like the ripe individuals from the beds off New Jersey that spawned before an abrupt temperature change.

The surf clam apparently develops its gonads to a ripe condition within a short period of time, contains ripe sex cells for several months of the year, and responds readily to relatively simple spawning stimuli. A rapid gonad development may account for the report by Carson (1945) that the surf clams of the mid-Atlantic coast spawn in the spring and throughout the summer. Allen (1951, 1953) obtained eggs of New Jersey coast clams from early spring to late autumn. Schechter (1941) collected ripe surf clams from areas near Woods Hole, Massachusetts, throughout the summer. Loosanoff and Davis (1963) found morphologically ripe eggs and spermatozoa in surf clam gonads from mid-January to the end of June. Conditioning the clams in the early months of the year by placing them in warmed water produced ripe specimens. Later in the season, when the natural waters had reached 12° C., no conditioning was needed, and thermal stimulation alone was sufficient to induce spawning. In contrast, other species of bivalves in the laboratory require various physical and chemical stimuli such as electrical shocks, rhythmic changes in water temperature, the addition of ammonium hydroxide to the water or injected into the gonad, or an introduction of egg or sperm suspensions to the water to induce spawning—and even then some species do not respond (Galtsoff, 1961, 1964; Loosanoff and Davis, 1963; Stickney, 1964).

The importance of nervous and hormonal interrelationships in bivalves has been reviewed by Galtsoff (1961, 1964) and Giese (1959). Products of neurosecretory cells inhibit spawning, and bivalves become sensitive to environmental spawning stimuli after the cells disappear. Degeneration of the neurosecretory cells begins a few days before spawning. Nagabhushanam (1963a) recognized two types of neurosecretory cells in the cerebral and visceral ganglia of *Spisula solidissima.* The cells in surf clams appear morphologically similar to those in the oyster, *Crassostrea virginica,* and the mussel, *Modiolus demissus* (Nagabhushanam 1963b, 1963c, 1964). Experiments with the latter two species link the cells with the hormonal control of the gametogenic cycle and spawning. Stimuli such as low salinities, electrical shocks, and high temperature influenced the secretions.

Both Galtsoff (1961) and Stickney (1964) believed that ripeness, rather than specific temperature, influences the response of some bivalves to spawning stimuli. Ripeness and sensitivity to spawning stimuli seem to precede the natural spawning period of surf clams by many months. I classified surf clams from New Jersey as ripe for at least two months each year before the first annual spawning. Some were induced to spawn in late May and early June, 1965, by simply placing them in running sea water aboard a research vessel. At four locations where the clams were caught, the water temperature increased as little as 9.5° C. and as much as 11.5° C. from bottom to surface. Changes in hydrostatic pressure or shocks from being caught by the jet dredge might stimulate spawning, but none of the clams from a fifth location spawned when the temperature change was only 0.8° C. A response to the stimuli of an abrupt change in temperature, well in advance of the seasonal time of spawning, suggests that the hormonal control of spawning can be overridden in surf clams. Nevertheless, a minimum temperature threshold for a spawning response is probably necessary.

Sections of surf clam gonads from geographic locations other than the commercial fishing areas off the New Jersey coast were examined, since a biannual reproductive cycle and spawning may not be typical throughout their range. In monthly samples from a more northern habitat—Sagadahoc Bay, Maine—during May through September, 1962, only a single reproductive cycle was apparent. Partially spawned and spent clams in the August and September samples were evidence of a late summer and early fall spawning.

In other bivalves, the reproductive cycle changes with latitude. Pfitzenmeyer (1962, 1965) and Shaw (1962, 1965) observed a biannual reproductive cycle in soft-shell clams, *Mya arenaria,* from Chesapeake Bay, Maryland, the southern part of their range. Ropes and Stickney (1965) reported on a single annual cycle in soft-shell clams from areas north of Cape Cod, Massachusetts, and discussed the available evidence of a biannual cycle and spawning south of Cape Cod. Porter (1964), who described the seasonal gonadal changes in hard clams, *Mercenaria mercenaria,* from North Carolina, found two annual spawning periods. Both of these species apparently have only one reproductive cycle each year, but two in southern waters. The change in the breeding season with respect to latitude and an extension of the season as one goes south has been observed in many temperate marine invertebrates (Giese, 1959).

I wish to gratefully acknowledge the cooperation of the members of the surf clam industry and many of the commercial fishermen who welcomed me aboard their vessels to sample clams from their catches at sea. The technical assistance of Virginia A. Liddell, Sally V. Otto, Brenda Spriggs, and Geraldine J. Fitzgerald aided me in the preparation of the many slides for the study. Dr. Rudolf S. Scheltema, Woods Hole Oceanographic Institution, Woods Hole, Mass., reviewed the manuscript and made many helpful suggestions. Dean F. Bumpus, Woods Hole Oceanographic Institution, Woods Hole, Mass., furnished the unpublished temperature records at Barnegat Lightship for 1964 and 1965.

SUMMARY

1. A biannual reproductive cycle was observed in *Spisula solidissima* gonads during 3 of the 4 years in which samples were taken from offshore New Jersey.

2. The biannual cycle was characterized by a major mid-year spawning and minor late-year spawning. A second annual reproductive cycle may be neither typical for surf clams throughout their geographical range nor always an annual event in clams from New Jersey.

3. A delayed spawning and single annual cycle in 1965 was related to colder environmental temperatures than were observed in the three earlier years of the study.

4. Abrupt temperature changes were not clearly a cause of spawning in the natural populations of surf clams. Partially spawned clams were found in the samples in advance of abrupt temperature changes. Temperature, however, clearly delays or hastens the gametogenic cycle and stimulates spawning of ripe surf clams in the laboratory.

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ABSTRACT

THE REPRODUCTIVE CYCLE OF SURF CLAMS FROM THE NEW JERSEY COAST

John W. Ropes

U. S. Bureau of Commercial Fisheries
Biological Laboratory
Oxford, Maryland

During the past 3 1/2 years nearly 2,500 gonad tissues of *Spisula solidissima* (Dillwyn) from the New Jersey fishery have been collected and processed for histological examination to determine the seasonal reproductive cycle. The adult clams, with a shell length of 120 mm or more, were caught by commercial hydraulic dredges in the vicinity of Barnegat Lightship, at water depths of 18 to 32 m. Samples of 25 clams were taken monthly in the winter and bimonthly during the spring, summer, and fall when active gametogenesis and spawning occur.

Five arbitrary categories were established to describe stages of the reproductive cycle. The time and duration of spawning is basic information necessary to understand the time of larval occurrence in the water and the eventual settling of juveniles on the bottom. The categories are: early active gametogenesis, late active gametogenesis, ripe, partially spent, and spent.

A biannual gamete maturation sequence culminating in the spent condition indicated that the clams had 2 spawning cycles each year. Spent gonads were collected in July and August and in mid-October, 1962 and 1963, and in July and August and early November, 1964. In 1965, a single maturation and spawning occurred in mid-September to late October. The delay in spawning and single annual cycle was related to the colder environmental temperatures not observed in the 3 earlier years of the study.

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THE TUNA RESOURCES OF THE OCEANIC REGIONS OF THE PACIFIC OCEAN

by

BRIAN J. ROTHSCHILD AND RICHARD N. UCHIDA

Introduction

This paper considers the tuna resources of the tropical and subtropical oceanic regions of the Pacific Ocean, the potential of these resources, and some of the constraints upon their complete utilization. We consider the tropical and subtropical oceanic region of the Pacific Ocean to be those areas of the high seas that are far from the continental land masses and lie between the approximate positions of the 20° C. isotherms. Thus only digressive consideration is given to the substantial tuna fisheries that are prosecuted in coastal or near coastal waters (e.g., the eastern tropical Pacific Ocean purse seine and live-bait fisheries for yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*)). For the tuna resources of the oceanic region we consider the location of the fisheries, the apparent effect of fishing on the abundance of each species, the trends in landings, and the potential of each fishery in terms of expected future yields both as to existing fisheries and those of future potential.

THE EXISTING TUNA FISHERIES

The tunas are the most important of the pelagic contemporaneously exploited resources of the Pacific Ocean. In the pelagic non-coastal areas, the largest catches of tunas are taken with deep-fishing longline gear. The three most important species taken by longline are the yellowfin tuna, the bigeye tuna *(Thunnus obesus)*, and the albacore *(Thunnus alalunga)*. The skipjack tuna is taken in lesser quantities, mostly at the surface with pole-and-line gear and with live bait as chum—although incidental catches are made by longline (see Miyake, in press). We consider first the tunas taken on longline gear and then the skipjack tuna taken with surface fishing gear.

The Longline Gear

The longline gear (Figure 1) is used principally to catch tunas. It is made up of units called "baskets." Each unit or "basket" consists of a mainline about 300 meters long. This mainline is suspended between two floats, and hangs in the shape of an approximate catenary. Four, five, or six equally spaced branch lines hang from each mainline. Each branch line is terminated by a sekiyama (cable wrapped with cotton thread), a wire leader, and a hook. The total length of the branch line and its terminal gear is about 20 meters. The usual bait used is the saury *(Cololabis saira)*. A typical set is composed of 400 baskets tied end to end, has a total of 2,000 hooks, and if stretched out would have a total length of 120 kilometers.

THE AUTHORS *were members of the scientific staff of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, at the time this article was written. Dr. Rothschild subsequently has become a member of the faculty of the College of Fisheries, University of Washington.*

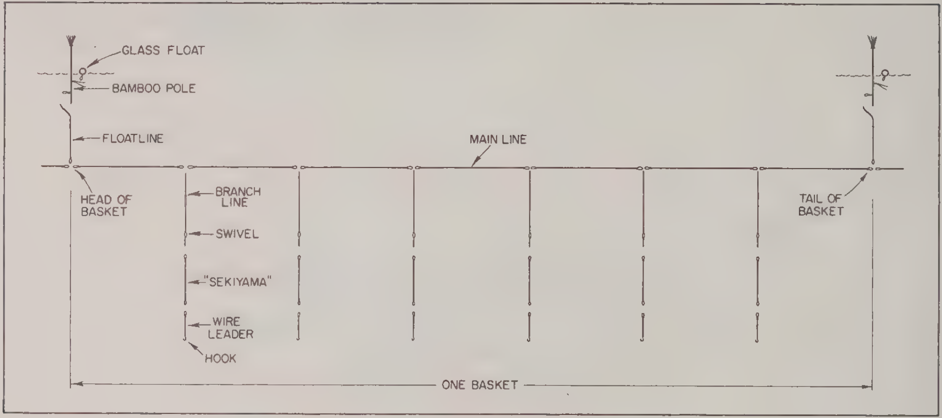

Figure 1.—Typical longline gear.

The Intensity and Distribution Of Fishing Effort

In this section we describe the substantial increases in Japanese longline fishing effort during the years following World War II. Particular attention is paid to the changes in temporal intensity and spatial distribution of the effort for bigeye tuna, yellowfin tuna and albacore. It is difficult to describe these changes on a species-specific basis because it is not uncommon to catch two or more species on the same set of longline gear—although there are more or less typical "grounds" (we identify these later) for each of the three species.

The spatial expansion of the Japanese longline effort was reported by Rothschild (1966a). He showed, using data from *Tuna Fishing,* that effort tended to be concentrated in the Western Pacific in the early 1950's; tended to move toward the central Pacific in the mid-1950's; and tended to be concentrated in the southeastern Pacific Ocean by the early 1960's (Figure 2). The distribution of effort in recent years (1963-65) is plotted in Figure 3; this effort distribution is based on that reported in the "Annual Report of Effort and Catch Statistics by Area on Japanese Tuna Longline Fishery, 1965" (Japan Fisheries Agency, 1967b), which we here call, for convenience, ARJTF. We can see from Figure 3, that the dynamic changes in effort have evolved into a contemporaneous distribution that is essentially concentrated into three general regions: (1) a region in the North Pacific centered on lat. 30° N. from the coast of Japan east to the date line, (2) an equatorial region in which effort tends to be concentrated to the north of the equator in the western Pacific and to the south of the equator in the eastern Pacific, and (3) a region off the east coast of Australia. As we shall see subsequently, the northern region is an albacore fishing ground in the west and a bigeye tuna ground in the east. Fishing in the equatorial grounds concentrates primarily on yellowfin tuna in the western Pacific and bigeye tuna in the eastern Pacific. Although we do not consider bluefin tunas in detail in this paper, the southern bluefin tuna *(Thunnus maccoyi)* is taken primarily on the fishing ground off the east coast of Australia and some northern bluefin tuna *(Thunnus thynnus orientalis)* are taken in the northern region.

The intensity of longline effort increased dramatically during the 1950's. This increase is reflected in the order-of-magnitude estimates of Otsu and Sumida (1966). These estimates as well as those given in ARJTF are shown in Figure 4. The cause of the discrepancy between the two sources is not immediately clear, but it is nevertheless evident that the intensity of longline fishing increased substantially during the 1950's. This substantial increase in the intensity of nominal effort implies that declines in the percentage of total annual effort expended in some regions are offset by increases in the absolute amount of nominal effort expended in these regions.

The Apparent Effect of Fishing

The severalfold increase in longline fishing effort generates interest in the relation between this increase and the yield potentials of the populations. The effect of the increased effort on the yield potentials can be gauged from correlations between the increase in effort and trends in the usual indices of population change: apparent abundance, average size, and total landings.

For the purpose of this paper it will suffice to consider changes in apparent abundance on a low-resolution 20° quadrangle per annum scale. Accordingly, the CPUE's (catch per unit of effort) for 1953 to 1963 for the yellowfin tuna, the bigeye tuna, and the albacore are plotted by 20° quadrangles for the entire Pacific Ocean in Figure 5. Figure 5 is adapted from Rothschild (1966a), which also contains a discussion of the interpretation of low-resolution longline data. Two features of Figure 5 are evident. The first concerns the location of the major fishing grounds for each species—which can be adjudged from the location of relatively high CPUE for the species. These regions are particularly noticeable in the early 1950's. These regions of relatively high CPUE identify a major fishing ground for yellowfin tuna in the equatorial western Pacific (long. 100° E.-180°, lat. 20° N.-20° S.); two major grounds for bigeye tuna—one in the North Pacific (long. 180°-120° W.) and another in the equatorial southeastern Pacific Ocean east of long. 140° W.; and two major grounds for albacore—one in the Northwest Pacific (long. 120° E.-180°, lat. 20°-40° N.) and another in the South Pacific

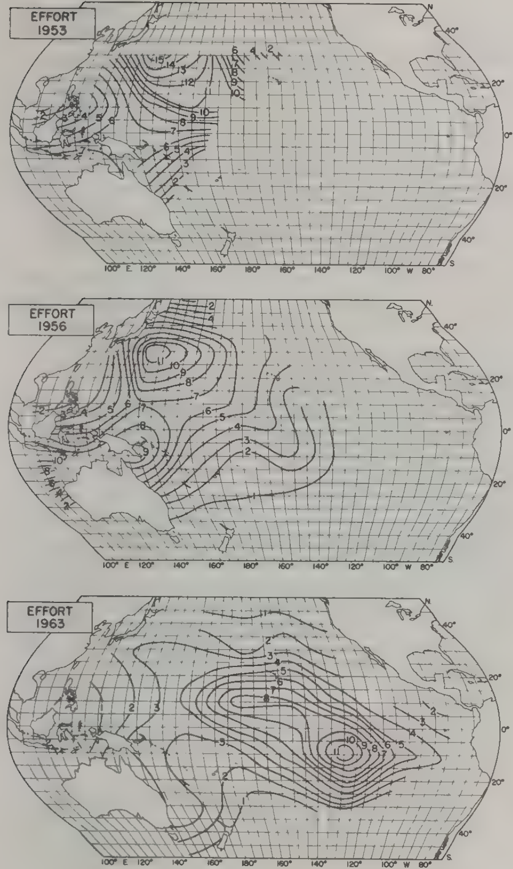

Figure 2.—Percentage of reported total annual effort (numbers of hooks) expended in each 20° quadrangle of ocean by the Japanese longline fleet for 1953, 156, and 1963 (after Rothschild, 1966a).

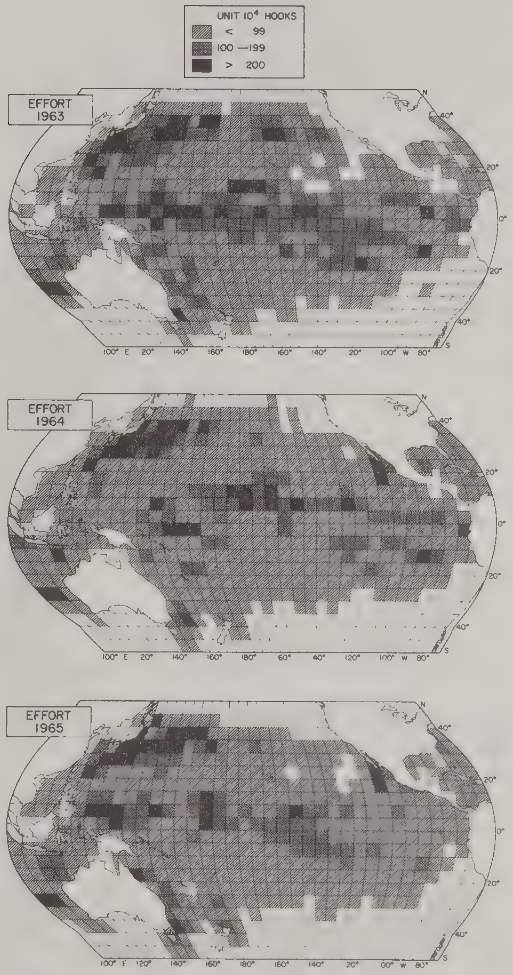

Figure 3.—Estimates of the distribution of Japanese longline effort based on ARJTF for 1963, 1964, and 1965.

east of long. 160° E. The second feature concerns the trends in apparent abundance for each species on its major fishing ground or grounds. Each species (with the possible exception of the albacore in the South Pacific), tended to decline in apparent abundance on its major fishing ground, particularly after the mid-1950's.

Another index that tends to reflect the exploitation status of a stock of fish is the difference between the average size of fish in the catch and the average size of fish at recruitment. If all other factors—such as growth rate, instantaneous coefficient of natural mortality, etc.—remain constant, then a reduction in the difference between the average size of fish in the catch and average size at recruitment corresponds to an increase in the instantaneous coefficient of fishing mortality—which means that fishing takes an increased proportion of the number of fish in a year class. There is clear evidence from the literature and from our studies that the average size of each species of tuna on most of the Pacific fishing grounds declined during the 1950's.

A possible exception to the general decline in average size for the three species under consideration is the albacore on the North Pacific longline grounds. For this fishery, Suda (1959) showed a decline in the average age of the fish in the catch. (If growth rate remains constant, a decline in average age is equivalent to a decline in average size.) Rothschild and Yong (MSa), however, could not find a corresponding decrease in the average size of the albacore taken on the North Pacific longline grounds. The reasons for this discrepancy are not known.

The albacore taken on the South Pacific albacore grounds exhibit decreases in average size which have occurred since 1956 at the beginning of the relatively intensive phase of this fishery (Otsu, 1966; Otsu and Sumida, MS).

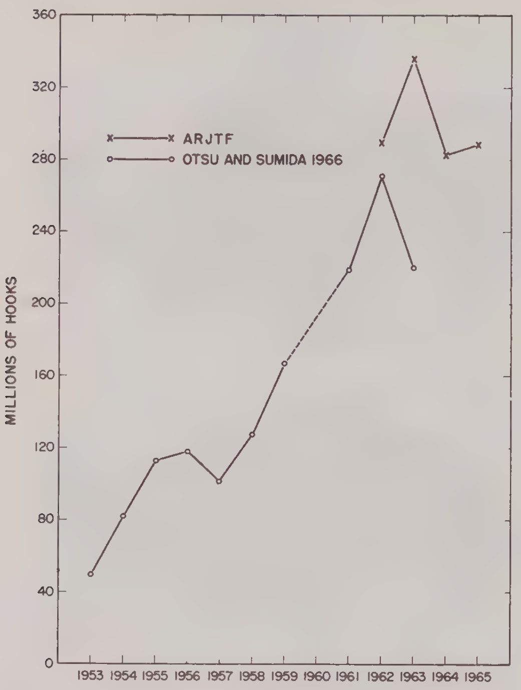

Figure 4.—Estimates of total number of hooks fished by the Japanese longline fleet in the Pacific Ocean from 1953 to 1965 based on estimates in Otsu and Sumida (1966) and ARJTF.

The yellowfin and the bigeye tuna both decreased in average size in the 1950's. As an example of these decreases, Rothschild and Yong (MSb) computed the difference between the average length of these two species in 1959 and 1954 (Figures 6 and 7). In the Christmas Island region, the average length of yellowfin tuna decreased from 140 centimeters in 1954 to 127 centimeters in 1959. This change corresponds to a reduction in average weight of about 13.6 kilograms (30 pounds). In the same region the average size of bigeye tuna decreased from 142 to 132 centimeters, which corresponds to a weight loss of about 11.3 kilograms (25 pounds).

The third index that reflects the exploitation status of the longline fishery is the total catch. Order-of-magnitude estimates of the total longline catch for each species are based on statistics compiled by Otsu and Sumida (1966) and are plotted in Figure 8. In the present discussion, each species is considered roughly in the order in which it became actively exploited. Thus, the fishing intensity of the longline fleet was most actively applied in the immediate post-World War II years to the albacore on the North Pacific albacore grounds. The catches of albacore soon reached a level of about 20,000 metric tons per year. With additional increments to total annual effort, fishing became concentrated in the equatorial western Pacific, where the yellowfin tuna was the most important species in the catch. The catch of yellowfin tuna tended to reach a level of about 65,000 tons in 1956. In 1956 the additional increments of total effort tended to be expended east of the date line in the South Pacific. As one correlate of this eastward expansion of effort, the South Pacific albacore catch increased sharply beginning in 1956. This increase resulted in elevating the total Pacific albacore catch of about 20,000 tons (caught mostly on the North Pacific grounds)

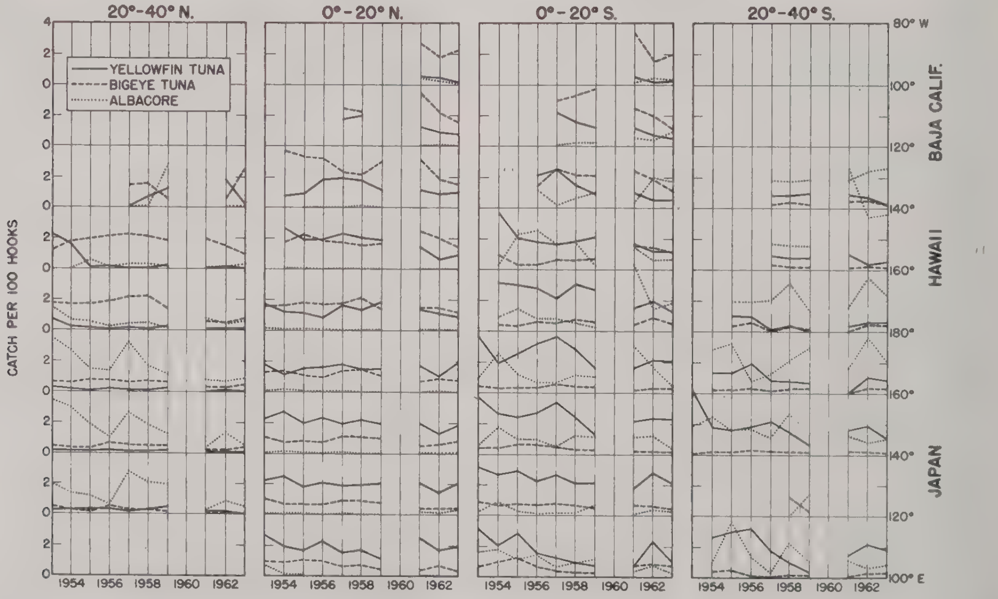

Figure 5.—Annual catch per 100 hooks for yellowfin tuna, bigeye tuna, and albacore for 20° quadrangles of the Pacific Ocean (based on Rothschild, 1966a).

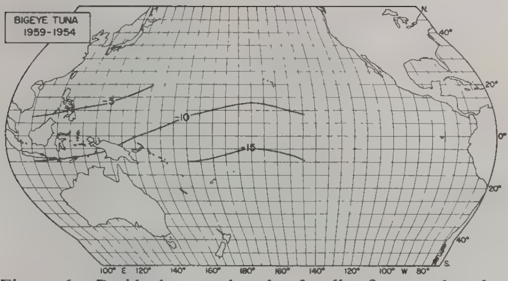

Figure 6.—Residual mean length of yellowfin tuna based on subtracting the estimated mean length of yellowfin tuna in 1959 from the estimated mean length of yellowfin tuna in 1954.

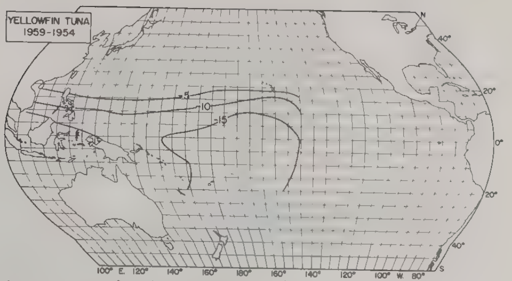

Figure 7.—Residual mean length of bigeye tuna based on subtracting the estimated mean length of bigeye tuna in 1959 from the estimated mean length of bigeye tuna in 1954.

to a level of about 50,000 tons. As a second correlate, bigeye tuna catches continued to increase as the fishery moved into the eastern Pacific—into areas of increasing apparent abundance of bigeye tuna. The eastward movement of effort reached the coasts of the Americas in 1963; at this time the bigeye tuna catch reached a level of about 100,000 metric tons.

Thus, on the basis of our rather qualitative examination, increasing total effort appears to be correlated with changes in apparent abundance, average size, and total catch for the three most important species of tuna that are taken on the longline gear. On the basis of our data all three species of tunas show declines in apparent abundance (with the possible exception of albacore in the South Pacific), declines in average size (with the possible exception of the albacore in the North Pacific), and a leveling or stabilization of total catch. On the basis of this qualitative examination it would seem that with the present method of fishing (with respect to gear, the size of fish that the gear selects, and the distribution and intensity of effort), substantial increases in the catches of yellowfin tuna, bigeye tuna, and albacore in the Pacific Ocean are unlikely.

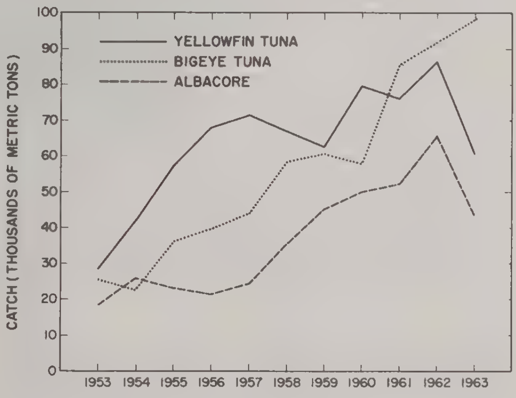

Figure 8.—Estimated Pacific Ocean catches of yellowfin tuna, bigeye tuna, and albacore, 1953-63 (based on Otsu and Sumida, 1966).

Skipjack Tuna Taken With Surface Gear

Several species of tunas are taken with surface gear in the pelagic non-coastal areas of the Pacific Ocean. The most typical species are the skipjack and yellowfin tunas, although neither species is taken in large quantities. Since catches of yellowfin tuna in the surface fishery are quite small when compared with catches of skipjack tuna, our discussion concerns primarily skipjack tuna.

In contrast to the highly dispersed longline fishery, the extant skipjack tuna fisheries and knowledge pertinent to potential skipjack tuna fisheries tend to be related to specific island groups (Figure 9). Owing to this circumstance, it will be most convenient to describe the surface fishing gear and then to describe the status of the skipjack tuna resource for those island groups where either a fishery operates or there is some knowledge about the skipjack tuna resource.

Surface Fishing Gear

The largest landings of tunas in the Pacific Ocean are taken with surface-fishing purse seines in the near-coastal skipjack and yellowfin tuna fisheries of the eastern Pacific. Some pole-and-line, live-bait gear is also used in the eastern Pacific, although this gear is much more typical in the Japanese near-coastal fisheries for albacore and skipjack tuna. In the non-coastal fisheries of the Pacific, the pole-and-line, live-bait fishing gear accounts for virtually the entire commercial catch of skipjack tuna.

One difficulty of pole-and-line and live-bait fishing for tuna is that it is basically two fisheries—a fishery for bait and a fishery for tuna. For the tuna fishery to be successful, the bait fishery must also be successful. After a fishing boat catches a load of bait it proceeds toward the fishing grounds in search of tuna schools. The fishermen usually do not search for the fish *per se*. Rather, they search for bird flocks that are associated with surface or near-surface schools of tuna. Upon sighting a flock of birds the fishermen set a course for the area where the birds are "working." When the fishermen reach the area some live bait is cast into the water. Not all schools feed on the live bait. Fish from feeding schools are caught by using a bamboo pole, a short line, and a metal jig. Catching fish by the pole-and-line and live-bait method requires a positive response from each of a lengthy sequence of events: The fishing boat must have bait, the fish school must be at or near the surface, birds must be present and see the school, the fishing boat must be in a location where birds are

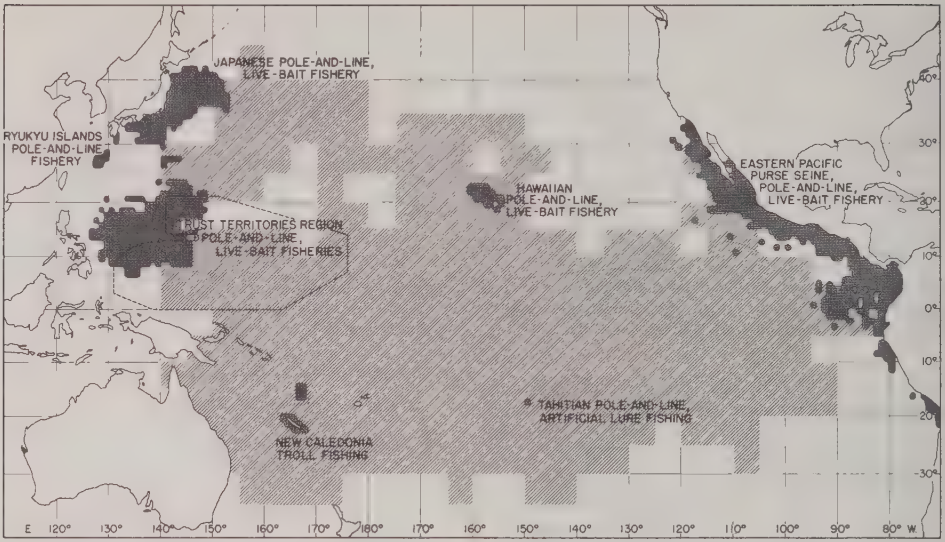
JAPANESE POLE-AND-LINE, LIVE-BAIT FISHERY
RYUKYU ISLANDS POLE-AND-LINE FISHERY
TRUST TERRITORIES REGION POLE-AND-LINE, LIVE-BAIT FISHERIES
HAWAIIAN POLE-AND-LINE, LIVE-BAIT FISHERY
EASTERN PACIFIC PURSE SEINE, POLE-AND-LINE, LIVE-BAIT FISHERY
TAHITIAN POLE-AND-LINE, ARTIFICIAL LURE FISHING
NEW CALEDONIA TROLL FISHING
40°
30°
20°
10°
0°
10°
20
-30°
E 120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80° W.

Figure 9.—The geographical location of skipjack tuna fisheries or fishing areas in the tropical Pacific as far west as long. 130° E. The lightly shaded area represents known locations where skipjack tuna have been taken on longline gear. The important Japanese pole-and-line, live-bait fishery and eastern Pacific purse seine and pole-and-line, live-bait fisheries are depicted (but not considered directly in the text). There are also small fisheries in Taiwan and the Philippine Islands.

aggregating over a school of fish, and the fish must bite. We suspect that, in general, the probability of obtaining a positive response from each event in this sequence is low.

It is clear, therefore, that the pole-and-line, live-bait fishing method relies heavily on the availability of live bait and the presence of bird flocks in the fishing areas. As a consequence much of the literature concerning the potential of non-fished areas for skipjack tuna refers to the frequency of bird-flock sightings and the bait resources of these areas. Therefore, we also discuss bait resources and the frequency of bird-flock sightings. It should be emphasized, however, that the latter index is affected by a large number of variables other than skipjack tuna distribution and therefore must be considered as a rather crude measure of abundance.

Commercial-Scale Fisheries

The Hawaiian fishery.—The Hawaiian skipjack tuna fishery uses pole-and-line gear and live bait exclusively. The wooden fishing boats are called sampans. The afterdeck is equipped with six baitwells arranged in two parallel rows. These baitwells also serve as stowage for the catch after the live bait is expended. The fishing power of the vessel is evidently related to baitwell capacity. Uchida (1967) called the smaller vessels of the fleet Class 1 vessels; these have baitwell capacities of 2,100-3,000 liters (550-800 gallons) per baitwell and registered lengths of 18-22 meters (58-72 feet). The larger vessels were called Class 2 vessels; these have baitwell capacities ranging from 3,000 to nearly 5,000 liters (800-1,300 gallons) and registered lengths of 20-25 meters (65-81 feet).

Information on the bait resources of Hawaii has been summarized by Nakamura and Iversen (MS). The most commonly used bait is a small anchovy *(Stolephorus purpureus)* called nehu locally. It made up 82 to 92 percent of all bait caught by the Hawaii tuna fleet from 1948 to 1960. Annual catches of bait were estimated to range from 21,676 buckets in 1960 to 47,937 buckets in 1955; the average catch for the 1948-66 period was estimated at 33,878 buckets per year. If the average weight of a bucket of bait is assumed to be 3 kilograms (7 pounds) then the maximum catch was about 150 metric tons per year. Fluctuations in the supply of nehu are apparently not related to fishing, but to other variables.

The nominal effort expended by the Hawaiian skipjack tuna fleet has been declining since the early 1950's (Uchida, 1967). The nominal effort in terms of fishermen-per-boat has declined from an average of about nine fishermen hooking per boat in 1950 to about seven in 1960. In addition the size of the fleet has dwindled from 27 boats fishing in 1950 to 17 in 1966.

Skipjack tuna fishing is restricted to within 90 miles of the main islands (Hawaii, Maui, Molokai, Oahu, and Kauai) in an area of about 181,000 square kilometers or 53,000 square nautical miles (Figure 10). Although the boats cover this extensive area, most of the effort is concentrated near Oahu—probably because most of the fleet is based at Oahu ports (13 in 1967, as compared with 2 at Maui and 2 at the island of Hawaii). For the 1948-65 period 50 percent of the catch was made in waters off Oahu, 28 percent in the waters off Maui, Molokai and Lanai, 13 percent in the waters off the island of Hawaii, and 9 percent in waters off Kauai and Niihau.

Many of the skipjack tuna caught in the commercial fishery in Hawaii are considerably larger than those taken in the eastern Pacific coastal fishery (Broadhead and Barrett, 1964, for the fishery in the northern part of the east-

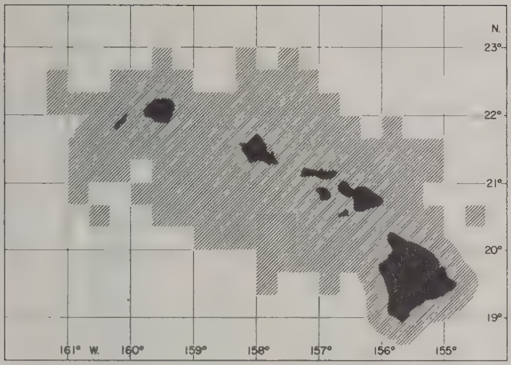

Figure 10.—Area within which Hawaiian skipjack tuna fleet fished (shaded) in 1948-65.

ern Pacific) and the Japanese coastal fishery (Kawasaki, 1955). The fish taken in the Hawaiian commercial fishery range in size from about 32 to 87 centimeters or about 1 to 17 kilograms (2-37 pounds). Brock (1954) showed that the lengths of skipjack tuna in the Hawaii catch comprised several modal groups. Rothschild (1965) showed that fish 60 to 70 centimeters long tended to be relatively common in the Hawaiian catches in years of high apparent abundance and relatively scarce in years of low apparent abundance. He interpreted this relation as a possible year-class-strength phenomenon. Rothschild (1967) reviewed the literature on skipjack tuna growth and provided growth estimates based on tagging data that would place the 60- to 70-centimeter fish at about 2 years of age.

The magnitude of the skipjack tuna catch from the Hawaiian fishery can be seen in Table 1 for 1900, 1903, and 1928-66, with the exception of 1943-44. Catches ranged from 1,434 to 3,594 metric tons in 1928-36, but rose to levels of 3,903 to 6,087 metric tons in 1937-40. Catches averaged nearly 4,600 metric tons in 1950-66 and ranged from 2,781 in 1957 to 7,329 in 1965 (nearly 2.5 times the 1957 catch).

The trends in fishing effort, in thousands of Class 2 trips; CPUE, in terms of tons of skipjack per Class 2 trip; and total catch, in metric tons are given in Figure 11. No striking long-term trends appear in catch, effort or CPUE.

Trust Territory region.—"The Trust Territory of the Pacific Islands has been under the trusteeship of the United States of America since July 1948. It is a vast area of 3 million square miles dotted with 2,100 islands of the Marianas, Palau, Yap, Truk, Ponape, and Marshall Islands Districts" (Rothschild, 1966c). The skipjack tuna resources of the Trust Territory region have a long history of exploitation. Since exploitation has not been confined to the present boundaries of the Trust Territory, however, our discussion concerns the general Trust Territory region.

The Japanese fishery for skipjack tuna in the Trust Territory region began in the early 1920's. Perhaps the best source of historical catch data for this fishery can be found in Shapiro (1948). Table 1 shows that the catches of skipjack tuna before 1930 were small and of little importance to the Japanese fishing industry; it was not until the mid-1920's that sufficient information, gathered from fishery exploratory research by the Japanese, indicated that important potentials for skipjack tuna fishing might exist in the Trust Territory—or the Japanese Mandated Islands, as the region was called before World War II (Smith, 1947; Shapiro, 1948). The skipjack tuna fishery expanded rapidly in the Trust Territory region in the 1930's. Peak production was in 1937—primarily due to the record catches made at Palau, Truk, and Ponape. Smith (1947) attributed the peak catch of 1937 to the operations of an unusually large number of fishing vessels, some of which were withdrawn the following year because of protests from Japanese producers and subsequent government restrictions on the number of skipjack tuna vessels that could operate in waters of the former Japanese Mandated Islands. Production reached a peak of 3,379 metric tons in Saipan in 1940, 149 metric tons in Yap in 1938, and 615 metric tons in Jaluit in the Marshalls in 1932. Lack of a readily available supply of live bait throughout the year limited production, particularly from Saipan (Ikebe and Matsumoto, 1938).

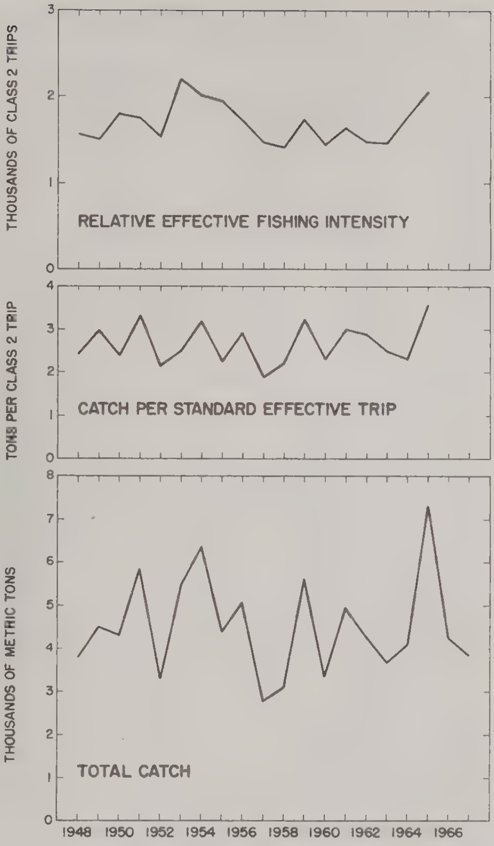

Figure 11.—Total catch, catch per standard effective trip, and relative effective fishing intensity in the Hawaiian skipjack tuna fishery, 1948-67.

A crude appraisal of the fishing effort expended in the

Table 1. Annual skipjack tuna catch in metric tons for various areas of the Pacific Ocean

Year	Eastern Pacific[1]	Hawaii[2]	French Polynesia[3]	Japan southern sea areas[4]	Landed in Samoa[5]	Saipan[6]	Yap[6]	Palau[6]	Truk[6]	Ponape[6]	Jaluit[6]	Japan[7]	Ryukyu Islands[8]
1900	–	191	–	–	–	–	–	–	–	–	–	–	–
1903	–	345	–	–	–	–	–	–	–	–	–	–	–
1917	190	–	–	–	–	–	–	–	–	–	–	82,795	–
18	1,372	–	–	–	–	–	–	–	–	–	–	70,091	–
19	3,128	–	–	–	–	–	–	–	–	–	–	64,395	–
1920	3,609	–	–	–	–	–	–	–	–	–	–	88,195	–
21	517	–	–	–	–	–	–	–	–	–	–	81,592	–
22	5,381	–	–	–	–	2	–	–	4	4	–	65,280	–
23	5,200	–	–	–	–	3	1	–	3	–	–	67,784	–
24	1,715	–	–	–	–	9	2	2	5	<1	–	68,275	–
25	6,457	–	–	–	–	15	2	9	6	5	–	69,536	–
26	9,523	–	–	–	–	45	2	42	3	<1	–	68,767	–
27	15,335	–	–	–	–	28	<1	15	8	2	<1	85,701	–
28	7,174	2,007	–	–	–	26	1	131	5	<1	–	76,987	–
29	12,246	1,514	–	–	–	25	<1	229	215	<1	–	72,135	–
1930	9,292	2,829	–	–	–	258	<1	157	913	6	–	68,789	–
31	7,488	2,777	–	–	–	564	<1	548	1,097	525	81	80,343	–
32	9,814	1,434	–	–	–	1,310	–	1,592	810	534	615	67,143	–
33	7,569	2,522	–	–	–	1,762	–	2,144	1,883	927	172	77,305	–
34	6,727	3,594	–	–	–	2,516	4	3,779	1,200	1,202	255	84,915	–
35	7,801	2,210	–	–	–	1,786	–	5,391	3,002	1,313	230	72,881	–
36	12,250	2,523	–	–	–	1,696	–	3,836	5,870	2,696	168	101,032	–
37	21,366	5,800	–	–	–	2,697	–	13,775	12,434	4,064	91	105,907	–
38	10,276	4,410	–	–	–	2,392	149	3,420	5,295	1,496	7	120,813	–
39	13,663	3,903	–	–	–	2,087	36	3,549	7,640	3,708	–	100,518	–
1940	26,118	6,087	–	–	–	3,379	4	6,047	7,217	1,586	<1	116,346	–
41	11,692	1,656	–	–	–	1,295	5	3,301	4,337	2,419	169	91,627	–
42	17,685	4	–	–	–	–	–	–	–	–	–	79,713	–
43	13,349	–	–	–	–	–	–	–	–	–	–	51,690	–
44	14,127	–	–	–	–	–	–	–	–	–	–	48,400	–
45	15,438	1,772	–	–	–	–	–	–	–	–	–	17,800	–
46	19,256	2,554	–	–	–	–	–	–	–	–	–	37,023	–
47	24,259	2,536	–	–	–	–	–	–	–	–	–	48,700	–
48	27,885	3,803	–	–	–	–	–	–	–	–	–	40,700	–
49	36,749	4,488	–	–	–	–	–	–	–	–	–	46,500	–
1950	58,634	4,314	–	–	–	–	–	–	–	–	–	84,600	–
51	54,948	5,863	–	–	–	–	–	–	–	–	–	104,300	–
52	41,179	3,308	–	–	–	–	–	–	–	–	–	86,000	–
53	60,626	5,470	261	–	–	–	–	–	–	–	–	72,700	–
54	78,805	6,360	324	–	–	–	–	–	–	–	–	99,800	–
55	58,061	4,397	279	–	6	–	–	–	–	–	–	99,700	–
56	68,176	5,050	500	–	2	–	–	–	–	–	–	98,000	–
57	58,197	2,781	500	–	1	–	–	–	–	–	–	97,500	4,056
58	74,799	3,100	400	–	–	–	–	–	–	–	–	147,400	7,064
59	80,559	5,631	500	–	–	–	–	–	–	–	–	166,700	10,958
1960	50,123	3,338	700	–	8	–	–	–	–	–	–	78,600	4,405
61	64,910	4,942	–	–	5	–	–	–	–	–	–	144,300	5,922
62	73,211	4,271	–	–	1	–	–	–	–	–	–	170,300	7,283
63	93,033	3,674	–	–	1	–	–	–	–	–	–	112,900	5,513
64	56,791	4,093	–	8,820	6	–	–	3,088	–	–	–	167,000	5,043
65	84,324	7,329	–	15,526	52	–	–	–	–	–	–	136,067	3,779
66	59,966	4,257	–	11,945	–	–	–	–	–	–	–	–	–

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[1] Data for 1917-33 are Power (1959: p. 383); data for 1934-54 are from Shimada and Schaefer (1956); data for 1955-66 are from Inter-American Tropical Tuna Commission (1967).

[2] Data for 1900, 1903, 1928-36 (fiscal years), 1937-42 and 1945-53 are from Yamashita (1958); data for 1954-66 are from catch records of the Hawaii Division of Fish and Game.

[3] Data for 1953-55 are from Van Pel and Devambez (1957); data for 1956-60 are from Food and Agriculture Organization (1966).

[4] Data for 1964 (June-December), 1965 (all months except May), and 1966 (January-April) are from Skipjack Fishing Ground Charts for the Southern Sea Areas, Tohoku Regional Fisheries Research Laboratory (no date).

[5] Data for Samoa are from records of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. Not shown in the table are landings at three ports in 1964: Santo, 7 metric tons; Noumea, 4 tons; and Fiji, 11 tons.

[6] Data for 1922-40 are from Shapiro (1948); data for 1941 are from Smith (1947); catch for Palau for 1964 is from Trust Territory of the Pacific Islands, 1965; [U.S.] Department of State (1965).

[7] Data for 1917-46 are from Espenshade (1948); data for 1947-64 are from Food and Agriculture Organization (1966); catch for 1965 is from Japan Ministry of Agriculture and Forestry (1967).

[8] Data for 1957-65 are from Mr. Jiro Isa, Economic Affairs Department, U.S. Civil Administration in the Ryukyu Islands.

Note: A catch of 235 metric tons was estimated from catches reported in Annual Report of Effort and Catch Statistics by Area on Japanese Tuna Longline Fishery, 1964, Japan Fisheries Agency (1967a).

Table 2.—Data on the catch of skipjack tuna in Palau district January-December, 1936 (based on Okajima, 1937)

Month	Catch			Average weight		Total trips	Number of boats fishing	Catch per trip		Catch per boat	
	Number of fish	Metric tons	Pounds	Kilograms	Pounds			Metric tons	Pounds	Metric tons	Pounds
Jan.	22,643	54.4	119,998	2.4	5.3	64	19	0.8	1,877	2.9	6,318
Feb.	5,738	8.7	19,186	1.5	3.3	26	9	0.3	736	1.0	2,134
Mar.	60,931	52.0	114,738	0.9	1.9	114	25	0.4	1,009	2.1	4,590
Apr.	169,444	187.9	414,228	1.1	2.4	313	30	0.6	1,323	6.3	13,811
May	399,334	560.6	1,235,852	1.4	3.1	585	32	1.0	2,109	17.5	38,621
June	295,382	480.6	1,059,618	1.6	3.6	612	30	0.8	1,728	16.0	35,321
July	129,081	257.9	568,612	2.0	4.4	343	26	0.8	1,654	6.2	13,596
Aug.	119,488	306.7	676,205	2.5	5.6	382	32	0.8	1,770	9.6	21,130
Sept.	110,556	348.8	769,069	3.2	7.0	396	31	0.9	1,943	7.5	16,540
Oct.	146,497	409.3	902,315	2.8	6.2	360	29	1.1	2,506	14.1	31,112
Nov.	241,122	730.2	1,609,681	3.0	6.7	518	30	1.4	3,110	28.9	63,656
Dec.	252,835	770.4	1,698,443	3.0	6.7	592	30	1.3	2,870	25.7	56,616
Total	1,953,051	4,167.5	9,187,945	2.1	4.7	4,305					

1930's in the Trust Territory region can be made from data presented by Smith (1947). He shows that there were 360 boats and 5,304 fishermen fishing in the Trust Territory in 1937. Most of the effort was concentrated in the Palau area. Intermediate amounts of effort were expended in the Truk, Saipan and Ponape areas.

Catch and effort statistics, given in Table 2 (Okajima, 1937), show that catches from the Palau district in 1936 totaled 4,168 metric tons on 4,305 trips, or an average of roughly 1 metric ton per trip. From the table, we also calculated that the vessels averaged 12 trips per month with a range from about 3 per vessel in February to about 20 per vessel in June and in December. The catch per trip tended to be seasonal, with peaks in May and November.

Commercial fishing in the Trust Territory region was halted with the onset of World War II, and was not resumed until the mid-1950's. In 1956, Van Pel (1956a) reported on a fishing venture for tuna in Guamanian waters. An old Japanese fishing vessel was refitted in Saipan for pole-and-line, live-bait fishing in July 1955. The vessel was 16.2 meters (53 feet) long and equipped with a 225 horse-power engine that propelled the vessel at a speed of 7 knots. The crew, recruited from fishermen skilled in pole-and-line, live-bait fishing, was from Saipan and Guam. The bait used was "aletses" *(Anchoviella purpurea)*. Fishing and scouting were confined within 1-4 miles of the islands and tuna schools were detected through the presence of bird flocks. Schools encountered were either skipjack or yellowfin tuna. The maximum catch was 1,700 pounds (about 0.8 metric ton) of skipjack and yellowfin tunas per day. After one trip aboard the Guamanian fishing boat, Van Pel stated that bait was insufficient and that the fishermen were inexperienced in bait fishing.

A sustained skipjack tuna fishery was initiated in the Trust Territory in 1964 when a small fleet began to operate out of Koror in the Palau Islands. Rothschild (1966c) described some of the plans and facilities. The initial planning provided for training of Micronesians as tuna fishermen on the Okinawan vessels that were to be operated out of Palau. The vessels, built in Okinawa, are about 25 gross tons each, with a length of about 65 feet (not including the catwalk) and a beam of 15 feet. Two baitwells, each holding about 30 buckets of bait are forward of the bridge, as are four ice holds and a fish hold. The vessels are powered by 6-cylinder, 90-horsepower engines and have a maximum speed of about 7 knots. Each vessel has 12 skilled Okinawan fishermen and 8 Micronesian trainees. It was intended that the trained Micronesians would eventually replace the Okinawans in the fishery. From August 1964 to June 1965 this fishery yielded 3,142 metric tons of skipjack tuna and 181 metric tons of yellowfin tuna (U.S. Department of State, 1966).

With respect to fishery development in the Trust Territory, however, the most dramatic recent increases in skipjack tuna effort and catch in the Trust Territory region have been made by the Japanese pole-and-line fleet. These increases can be ascertained from the "Atlas of Skipjack Tuna Fishing Grounds in Southern Waters 1964 and 1965" published by the Tohoku Regional Fisheries Research Laboratory.

The atlas is based primarily on interview records obtained by a branch office of the Tohoku Laboratory at the Port of Yaizu (Yaizu, in Shizuoka Prefecture, is a major Japanese port for landing fish taken in the Trust Territory region). Table 3 is based on the atlas and shows estimates of the number of vessels fishing for skipjack tuna in the Trust Territory region south of lat. 24° N. and the estimated catches of these vessels from June 1964 to April 1966. The data from Table 3 are plotted in Figure 12, which shows that there is considerable fluctuation in the number of vessels fishing. The number is highest in March; it tends to be low in April, May, and June because Japanese coastal spring live-bait fishing for albacore is at its annual peak during these months. Since albacore bring a higher price than skipjack tuna, most of the effort shifts to albacore. The depression of effort in January is related to the Japanese several-week New Year holiday. Landings tended to be correlated with the amount of effort. The landings per boat, a rough measure of apparent abundance, tend to exhibit two peaks during the year, in August-September and February-March. Apparent abundance tends to be depressed in October-December and in April-June. The peaks in August-September and February-March correspond with the data given by Okajima (1937) for the 1936 season in the Palau district (see Table 2).

The atlas shows significant seasonal changes in the location of fishing and in the size distributions of the

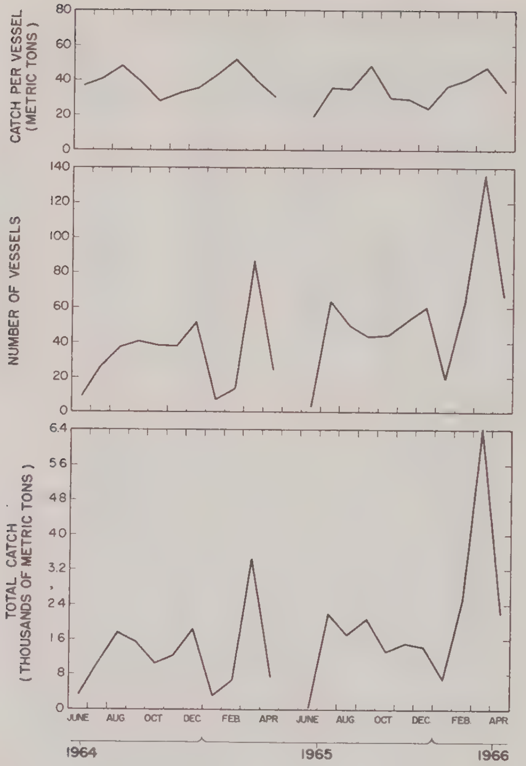


Figure 12.—Estimated number of fishing vessels, total catch of skipjack tuna, and catch per boat for the Trust Territory region June 1964-April 1966. (Data are from Table 3.)

catch. In June-September fishing tends to be concentrated near the Marianas and the distribution of the catch tends to be oriented north-south. In October or November the distribution of catches tends to move to the southwestward and in January-March (the peak fishing period) the catches are clearly oriented east-west—possibly along a frontal system associated with the North Equatorial Current, roughly at lat. 10°-15° N., long. 125°-145° E. There are, then, two clearly defined fishing areas: one in the Marianas in the summer and another between the Philippine Islands and the Marianas, roughly between lat. 10° and 15° N. These two areas are shown in Figure 13 using as an example the distribution of catches in September 1965 and February 1966. The atlas also presents some size distributions. In the Marianas grounds in 1964 the most common size of fish was between 40 and 50 centimeters. When fishing shifted to the north equatorial area the typical size increased to 50-60 centimeters. In 1965 the typical size in the Marianas grounds was 50-60 centimeters. Thus, the fish taken on the Marianas grounds in 1965 were larger than in 1964, but in both years the size of fish taken on the north equatorial grounds was about 10 centimeters larger than the size of fish taken in the corresponding year in the Marianas area.

Table 3.—Estimated number of vessels that fished for skipjack tuna in the southern sea areas, total landings, and landings per vessel, June 1964-April 1966

Year	Month	Number of vessels	Landings of skipjack tuna (metric tons)	
			Total	Per vessel
1964	June	9	328	36.5
	July	26	1,051	40.4
	Aug.	37	1,771	47.8
	Sept.	40	1,559	39.0
	Oct.	38	1,044	27.5
	Nov.	38	1,215	32.0
	Dec.	52	1,852	35.6
1965	Jan.	7	305	43.6
	Feb.	13	667	51.3
	Mar.	86	3,443	40.1
	Apr.	24	735	30.6
	May	–	–	–
	June	3	58	19.3
	July	63	2,225	35.3
	Aug.	49	1,724	35.2
	Sept.	43	2,084	48.4
	Oct.	44	1,312	29.8
	Nov.	52	1,528	29.4
	Dec.	60	1,445	24.1
1966	Jan.	19	702	36.9
	Feb.	63	2,547	40.4
	Mar.	136	6,484	47.5
	Apr.	66	2,212	33.5

Table 4.—Average lengths of skipjack tuna caught in Palau waters in summer and in winter, 1965-67

Period	Average length (centimeters)
May-September 1965	51.8
October-November 1965; January 1966[1]	58.9
May-September 1966	57.4
October-December 1963; January 1967	59.3
May-September 1967	54.4
October-December 1967	57.6

[1] No data for December 1965.

This same size difference was evident in the skipjack tuna caught in Palau waters in 1965-67, although the differences in the average sizes between summer and winter for these years were not as great as shown for the north equatorial and Marianas grounds. Table 4, which shows the average lengths of skipjack tuna taken in the summer (May-September) and in the winter (October-January) in Palau indicate that in 1965 there was a difference of about 7 centimeters between the average sizes caught in the summer and winter. In 1966-67, the size differences between summer and winter were roughly 2 to 3 centimeters. Skipjack tuna were also conspicuously larger in the summer catch of 1966 than in the summer catches of 1965 and 1967. These observations, along with three recent recoveries near Yap of skipjack tuna tagged in Palau, suggest that the skipjack tuna taken in Japanese fisheries of the Trust Territory region and those taken in the Palau fishery are a common stock.

The expansion of pole-and-line fishing in the Trust Territory region will naturally depend on the bait resources of the region. The present Japanese fishery for skipjack tuna in the Trust Territory region apparently

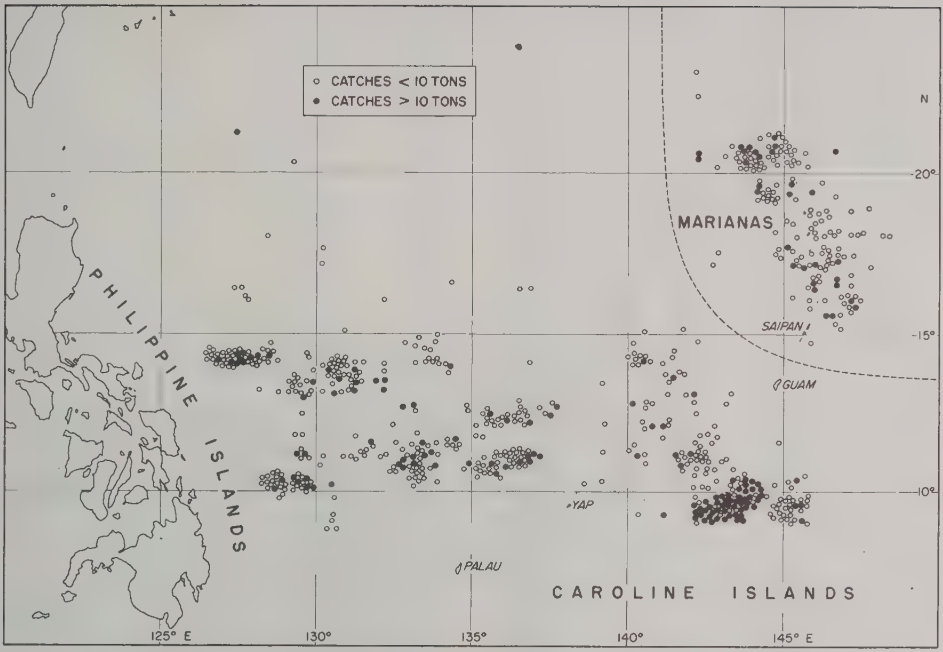


Figure 13.—Representative catches of skipjack tuna in the Trust Territory region as reported in the atlas of the skipjack tuna fishing grounds. Data northeast of the dashed line are from the "summer" fishery, September 1965. Data southwest of the dashed line are from the "winter" fishery, February 1966.

utilizes bait carried to the fishing grounds from Japanese waters, but the pre-war Japanese fleet fishing in the Trust Territory region was based there entirely, and therefore must have used bait caught in Trust Territory waters. A rough estimate of the extent of the contemporaneous bait resources in the Trust Territory can be made if it is assumed that the fluctuations in the catch of skipjack tuna in the pre-World War II years were independent of bait abundance and the quantity of bait is computed for 1937, the year in which the Trust Territory catch of skipjack tuna was maximal. Such an estimate was made by Nakamura and Iversen (MS) by further assuming that the catch of skipjack tuna per bucket of bait is roughly the same as that for Hawaii (122.4 kilograms or 270 pounds of skipjack tuna per bucket of bait). This estimate suggests that the 1937 Japanese fishery used 112,000 buckets of bait, which is almost certainly more bait than is now being taken in the Trust Territory. We do not know, however, if this quantity of bait could be taken on a sustained basis, or how it is distributed among the islands (although it is likely that most of the bait was taken at Palau).

Small-Scale Fisheries and Unexploited Areas

In this section we consider the areas without extensive commercial fisheries for skipjack tuna. These include the Leeward Islands, the Line and Phoenix Islands, Samoa, French Polynesia, Cook Islands, and New Caledonia. We also consider the rather incidental catches of skipjack tuna made by Japanese longline vessels. In addition we try to consider not only the skipjack tuna, but the frequency of bird-flock sightings (which may be indicative of the abundance of skipjack tuna), and the bait resources.

Leeward Islands.—The Leeward Islands consist of about 17 banks, reefs, and islands. They extend northwestward from Kauai in the Hawaiian chain to Midway Island. This chain of islands and shallow-water banks has some very productive baiting grounds, such as French Frigate Shoal (Smith and Schaefer, 1949; Eckles, 1949; June, 1951). The main species of bait at French Frigate Shoal is the silverside *(Pranesus insularum)* or iao as it is called by Hawaiian fishermen. The silverside is a very hardy baitfish which is suitable for long-distance transport in the baitwells of fishing vessels. June and Reintjes (1953) stated that this is the best baitfish in the Leeward Islands, but that its abundance apparently fluctuates markedly at various places in the Leeward region.

Although there is now no commercial production of skipjack tuna from the Leeward Islands, there are sufficient reports of tuna school sightings—based on several exploratory fishing cruises—to indicate possible commercial concentrations of yellowfin tuna, skipjack tuna, and little tuna *(Euthynnus affinis)*. According to Waldron (1964), the rate of bird-flock sightings in the Leeward Islands was highest in March-May and again in June-August—periods which coincide with the skipjack tuna fishing season in Hawaiian waters. The rate of sightings from the Leeward

Table 5.—The number of hours scouted and number of fish schools sighted in the region of the Line and Phoenix Islands during seven cruise periods in 1950-51

Year and period	Island	Hours scouted	Number of schools sighted				
			Skipjack tuna	Yellowfin tuna	Unidentified	Mixed species	Total
1950							
4/22-6/7	Line	310	8	12	5	3	28
7/24-9/1	Phoenix	64	4	2	5	–	11
9/2-9/19	Line	85	–	8	6	–	14
11/1-12/1	Line	226	7	9	6	–	22
1951							
1/24-2/5	Phoenix	29	–	–	4	–	4
2/11-2/23	Line	104	2	1	–	2	5
4/5-5/12	Line	208	2	2	2	–	6
Total		1,026	23	34	28	5	90

Islands region was similar to that for Hawaiian waters and was sometimes considerably higher.

Line Islands and Phoenix Islands.—Our knowledge of the skipjack tuna and bait resources of the Line and Phoenix Islands is based largely on exploratory cruises made to the area by research vessels of the Bureau of Commercial Fisheries Biological Laboratory at Honolulu.

On cruises of the *Oregon, N. B. Scofield,* and *Calistar* to the Line Islands in 1948-49, numerous schools of skipjack and yellowfin tuna were seen, particularly near the islands (June, 1951). Civil Aeronautics Administration personnel stationed at Palmyra at that time confirmed that tuna schools are close to the island throughout the year. June concluded that schools of skipjack and yellowfin tuna can be expected to occur in waters of the Line Islands in sufficient numbers for commercial exploitation. He also concluded that skipjack and yellowfin tuna are present in commercial quantities off Canton Island in the Phoenix group, but their relative abundance at different times of the year is not known.

A series of cruises was also undertaken in 1950 and 1951 to the Line and Phoenix Islands area. Table 5 summarizes the results of scouting for surface schools of skipjack and yellowfin tuna in terms of the number of hours scouted and the number of fish schools observed. In 1,026 hours of scouting, 90 schools were sighted, of which 26 percent were identified as skipjack tuna, 38 percent as yellowfin tuna, and 31 percent were unidentified.

According to the summary of bird-flock and fish-school sightings prepared by Waldron (1964), the rate of sightings of bird flocks near the Line Islands appeared to be higher than in the Phoenix Islands area in December-February, but lower during the rest of the year. The rate of bird-flock sightings appeared to be particularly high in the Phoenix Islands area in June-August and September-November. Waldron's analysis also permits a comparison of bird-flock and school sightings among regions. He shows that the frequency of sightings of bird flocks, skipjack tuna schools, and total fish schools apparently was somewhat lower for the Line Islands than for the Hawaiian or Marquesas Islands.

Very little is known about the bait resources of this area. In an account of tuna and bait resources of the Line Islands, June (1951) pointed out that species suitable for bait, such as mullet *(Mugil crenilabis, M. vaigiensis,* and *M. trichilus), milkfish *(Chanos chanos),* and goatfish (sp.?) were fairly abundant on Palmyra Island. June and Reintjes (1953) also made the observation that species suitable for use as supplemental live bait were available in the lagoon at Fanning Island and that Christmas Island was potentially the most important baitfish source in the entire Line Islands chain. Concerning islands in the Phoenix group, they concluded that stocks of baitfishes present at Canton Island were only fair as tuna bait. It was also noted that stocks of mullet, which can be used for livebait fishing, fluctuated in abundance throughout the year. At Hull Island several species of mullet occurred in varying abundance, but probably not in sufficient quantity to sustain a commercial fishing operation.

On the basis of experimental fishing with purse seines in the Line-Phoenix Islands area in 1950 and 1951, Murphy and Niska (1953) concluded that purse seining for tuna in the Line Islands was a problematical venture because of the wildness of the schools or because of the proximity of many of the schools sighted to reefs; in the Phoenix Islands the prevailing high winds limited purse seining to the lees of the islands where schools of tuna were relatively scarce and frequently too close to the reefs for effective purse seining.

Samoa.—In 1949, a company called Island Packers, Inc., installed a small tuna cannery on Tutuila Island, American Samoa. Attempts to keep the cannery supplied with fish caught near Samoa, through pole-and-line, livebait fishing and purse seining, however, ended in failure. Since then, several companies have initiated sustained processing operations, utilizing fish caught and landed in Samoa by foreign longline vessels (Van Campen, 1954).

Skipjack tuna occur in waters around Samoa, but their abundance and distribution are not known. Suitable bait species also occur in Samoan waters, but it is not known whether the supply is adequate for sustained commercial fishing.

In a summary of fish schools and bird-flock sightings in the central Pacific near Samoa, Waldron (1964) showed that sightings of bird flocks averaged 4.23 per hour in December-February (26 hours of scouting). This figure compares favorably with the sightings of bird flocks in the Hawaiian area during June-August, when skipjack fishing is at its peak. Data on bird-flock sightings were not available from the Samoa area for other periods of the year.

French Polynesia.—The Marquesas, the most north-

Table 6.—Number of tuna schools chummed, the number and percentage successfully fished, and the average number, average weight, and average catch per school for pure and mixed schools of skipjack and yellowfin tuna, Marquesas Islands, 1956-59

Year	Number of schools chummed	Schools successfully fished		Skipjack tuna			Yellowfin tuna		
				Average number per school	Average catch per school	Average weight	Average number per school	Average catch per school	Average weight
		(number	(percent)		(metric tons)	(kilo-grams)		(metric tons)	(kilo-grams)
1956	10	2	20	344	1.4	4.1	1	–	–
1957	155	53	34	142	0.4	3.2	20	0.2	6.6
1958	127	42	33	91	0.3	4.2	5	<0.1	6.2
1959	153	52	34	76	0.3	3.9	32	0.5	13.3

easterly of the islands of French Polynesia, are high islands of volcanic origin, lying about 2,080 nautical miles southeast of the Hawaiian Islands. In 1954, the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, surveyed the tuna and bait resources of the Marquesas (Royce, 1954). In 1956-59, 10 exploratory fishing or oceanographic cruises were made to the Marquesas-Tuamotu-Society Islands and 1 commercial fishing venture was started. Some of the results have been reported by Austin (1957), Wilson and Rinkel (1957), Wilson and Austin (1957, 1959), Wilson, Nakamura, and Yoshida (1958), and Yoshida (1960). The results showed ample indications of tuna, but not a sustained abundance of the most common baitfish, the Marquesan sardine (*Sardinella* sp.).

Sightings of working bird flocks were numerous in the Marquesas. Royce (1954) reported good catches of tuna, but there were also many wild schools from which few or no fish were caught.

Wilson and Austin (1959) summarized school sightings from the Marquesas for 1957-58. In 107 days of scouting, the Bureau's research vessels sighted 573 schools, or an average of about 5.4 schools per vessel per day. The density of schools was higher, however, during the Marquesan summer (January-March). For example, in 1958, for the periods January 18-25 and February 27-March 5, 174 schools were sighted in 15 days of scouting, or an average of 11.6 schools per vessel per day. This is more than twice the number of sightings per vessel per day in Hawaiian waters; during 240 days of scouting divided among seven commercial sampans in Hawaii 1,252 schools were sighted in June-August 1967—or an average of 5.2 per vessel per day. The differences in the rate of bird-flock and tuna-school sightings between the Hawaiian and Marquesan regions can also be seen in Waldron (1964).

The percentage of schools successfully fished in the Marquesas in 1956-59 appears to be rather low compared with the percentage of success experienced by Hawaiian skipjack tuna fishermen. Table 6 gives a summary of the number of tuna schools chummed, the number and percentages that were successfully fished, and the average number, average weight, and average catch per school for skipjack and yellowfin tuna. If we discount the value given for 1956 because of the small number of schools fished and use only data for 1957-59, it is evident that only about one-third of the schools chummed are successfully fished. This low rate of success appears to substantiate the findings of Royce (1954) and other investigators who have commented that the schools in Marquesan waters are wild and fast-traveling.

In contrast, the percentage of success is much higher among the Hawaiian skipjack fishermen. Yuen (1959) reported that 48 percent of the schools chummed yielded fish, Royce and Otsu (1955) concluded that 43 percent of the schools which were approached and chummed with live bait came close enough to the vessel for some fish to take the hook. Additional observations on the Hawaiian fleet in the summer of 1967 indicated that during the skipjack tuna fishing season the percentage of schools successfully fished was 51 percent in June, 68 percent in July, and 59 percent in August.

The catch per school in Marquesan waters (<0.5 metric ton per school) was considerably less than that in Hawaiian waters. In Hawaii, estimates of catch per school averaged about 1.0 metric ton for inshore schools (within 37 kilometers or 20 miles of the islands), and about 1.5 metric tons for offshore schools (Uchida, MS). The small catch per school in Marquesan waters, however, may be related to fishermen aboard the research vessel fishing at a slower rate to accommodate certain scientific operations.

Of 2,208 skipjack tuna caught from surface schools of skipjack and mixed skipjack-yellowfin tuna in the Marquesas Islands in 1957-59 (Figure 14), the smallest fish measured about 39 centimeters (1.1 kilograms or 2.5 pounds) and the largest was 83 centimeters (14.4 kilograms or 31.7 pounds). Most of the fish, however, meas-

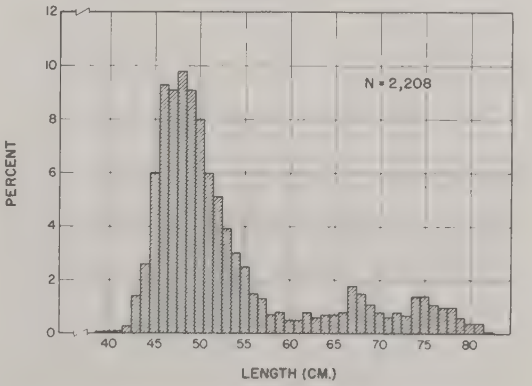


Figure 14.—Length-frequency distribution of skipjack tuna caught by pole-and line, live-bait fishing in the Marquesas Islands, 1957-59.

ured from 45 to about 55 centimeters (1.8 to 3.6 kilograms or 4 to 8 pounds).

Next we consider the Society Islands, which comprise both Windward and Leeward Islands. Tahiti, in the windward group, is the only island with commercial production of skipjack tuna. The discussion of the fishery by Van Campen (1953) and Van Pel and Devambez (1957) is the source of the following account.

The Tahitian tuna fishing boats are rather small, ranging in length from 6 to 7.6 meters (20 to 25 feet), with a beam of 2-2.3 meters (6.5-7.5 feet) and a draught of about 0.6 meter (2 feet). The craft closely resemble small sportfishing cruisers in general appearance. The boats have a small deck and roofed-over cabin forward and an after cockpit. Diesel engines rated at 15-20 horsepower propel the craft at 6-8 knots. Usually, two to three fishermen fish from each boat. About 20 such boats are actively engaged in skipjack tuna fishing. The fishing gear consists of a 4.6-meter (15-foot) pole with one or two cotton lines attached; a wire leader and an artificial lure made of pearl shell, metal, metal and feathers, or horn and feathers, and a barbless hook. The boats usually operate within 56 kilometers (30 nautical miles) of Tahiti. They depart for the fishing grounds at about 0800 hours and return between 1700 hours and midnight.

As in many other areas where a skipjack tuna fishery exists, schools are located by bird flocks. When fishing, the boat is kept under way and moving with the school. The fishermen then slap and drag the lure on the surface of the water until a fish strikes. When fish are not biting, the fisherman changes lures by switching to the second line attached to his pole, or tying a different lure to the line, to find the one that is most productive. The hooked fish is lifted out of the water and swung into the cockpit, somewhat like the "flipping" method of pole-and-line, live-bait fishermen of the eastern Pacific and Hawaii. The fishermen try to unhook the fish while it is in the middle of its trajectory so that the lure can be returned to the water rapidly.

Live bait is never used in fishing. Sprays and splashing of waters, which are commonly used by skipjack tuna fishermen elsewhere in the Pacific, are not used by Tahitian fishermen, but occasionally Tahitian fishermen drag banana or coconut palm leaves through the water to attract the ature or bigeye scad *(Selar crumenophthalmus),* which take refuge under the boat and attract skipjack tuna toward the stern. Fishing in this fashion increased the yield considerably (Angot, 1960). Small pieces of fish are sometimes thrown out to attract the tuna.

The skipjack tuna fishing season is in December-March and July-August, but usually some fish are caught during other months of the year. Individual boat catches are highly irregular; a good day's catch is said to be about 20-30 per boat, but catches may be as high as 200. On the average, the fish range from 2.7 to 4.5 kilograms (6 to 10 pounds). There have been unconfirmed reports of very large skipjack tuna being taken in Tahitian waters.

The annual catches range between about 200 and 500 metric tons or (on the basis of 20 boats) 10 to 25 metric tons per boat per year.

A small cannery, established in 1939 to pack pineapple, was converted to processing tuna, but ceased operations in 1947.

Cook Islands.—Until 1965 the now-independent Cook Islands were administered by the Department of Island Territories of the New Zealand Government, at Wellington, through a Resident Commissioner who had headquarters at Rarotonga (Tudor, 1963).

A small subsistence fishery for skipjack and other tunas and Spanish mackerel is carried on in the Cook Islands. These islands are widely scattered over an area of about 850,000 square miles extending from lat. 9° to 23° S., between long. 156° and 167° W. (Van Pel, 1955). Canoes are used in the fisheries and activities are confined to areas near the coast. Handlining and trolling are the main methods used (Van Pel, 1955).

New Caledonia and dependencies and the Condominium of the New Hebrides.—Van Pel (1956b) has stated that in spite of the abundance of flyingfish in the offshore waters, deep-sea fishing accounts for negligible catches in waters of New Hebrides. Some sport fishing is carried on in these waters and some tunas, billfishes, Spanish mackerel, barracuda, and dolphin have been taken. Japanese longliners also fish close to these islands and land their catch at Santo and Nouméa in New Caledonia. Van Pel also observed some surface schools of small tuna and skipjack in the vicinity of Port Sandwich and in waters south of the island of Malekula in the New Hebrides group.

Surveys of waters in the vicinity of New Caledonia, Loyalty Islands, and New Hebrides showed that trolling gear was suitable for taking schools of skipjack and yellowfin that were near enough to the surface close to land (Angot, 1959). The main species taken was the yellowfin tuna. They averaged about 8.2 kilograms (18 pounds) although some as large as 45.4 kilograms (100 pounds) were also taken. Most were taken just outside the reef and in the passes, but sometimes well within the lagoon. Skipjack tuna were usually taken farther offshore and they averaged 2.7 kilograms (6 pounds) and seldom exceeded 9.1 kilograms (20 pounds). Catches of these fishes by the research vessel *Orsom III* were frequently quite satisfactory; for example, 1.4 metric tons (1.5 short tons) were caught in less than 24 hours off St. Vincent, Uitoe, and Isie Passes in February 1956; a catch of 0.4 metric ton (820 pounds) was made in a few hours off Bourail in May 1957; 1.3 metric tons (1.4 short tons) were taken in 1 day near the northwest coast of Lifou in August 1957; and 0.3 metric ton (700 pounds) in a few hours between La Havannah and the Woodin Canal in January 1958.

A commercial trolling fishery for tuna has been established in New Caledonia. The catch, according to Angot (1959), is sufficient to supply the demand of the Nouméa market. Description of the trolling cutters, type of gear, and its installation can be found in Criou (1959).

POTENTIALS OF TUNAS

In considering the potential of the tuna resources we shall examine the possibility of increased yields with present fishing methods, the possibility of increased yields under modification of present fishing methods, and the distribution of apparent abundance or CPUE and catch for the comparatively recent years of 1962-65.

Yellowfin Tuna

We showed that declines in apparent abundance, average size, and a stabilization of yield at about 65,000 tons per year suggest that substantial increase in catches of yellowfin tuna under the present longline fishing structure is unlikely. This conclusion is corroborated by more detailed studies which have been synthesized by Kamimura (1966). Kamimura concluded that the fishing intensity for yellowfin tuna rose to an extremely high level in 1962 and that increases in effort beyond the 1962 level would not increase the catch.

Thus, optimization of yellowfin tuna exploitation in the central Pacific Ocean can be considered from two viewpoints. First, it is possible that a manipulation of fishing intensity or recruitment size would result in higher yields than those now obtained; second, it may be possible to develop methods to increase the efficiency of the present fishery and thus, without necessarily increasing total yield, achieve improved wage and price structures and free units of effort to fish for other species.

With respect to manipulating fishing intensity or recruitment size to increase yield-per-recruit, Murphy and Pella (1966) noted that a reduction in recruitment size in the longline yellowfin tuna fishery of the central Pacific would result in increasing the yield-per-recruit by 30-50 percent. Their conclusion was based on the reasonable—for a first approximation—assumption that the vital rates estimated by Hennemuth (1961) for yellowfin tuna taken in the eastern Pacific surface fishery would be applicable to yellowfin tuna taken by the longline fishery in the central Pacific. On the basis of recent estimates of fishing intensity (Kamimura 1966: 769) and recruitment size for the western Pacific, however, it does not appear that substantial increases in the catch would result from a reduction in recruitment size.

To utilize fully the concepts of yield-per-recruit for the management of the yellowfin tuna in the central Pacific we would need to manipulate fishing intensity and size at recruitment. Methods of manipulating fishing intensity are obvious (but possibly not always practicable). Methods of manipulating size at recruitment for the longline fishery are not as immediately apparent. The usual way of manipulating the size at recruitment is to modify the selectivity of the gear. The selection properties of longline gear are not well understood, but nevertheless we can make some observations which might be applicable to manipulating the size at recruitment for yellowfin tuna in the central Pacific.

The first observation on the possibility of manipulating size at recruitment concerns the increase in average size of yellowfin tuna from west to east along the equator (see e.g., Murphy and Shomura, 1955). This increase in size has been explained as a reflection of yellowfin tuna migrations from the western to eastern portions of the Pacific Ocean (see Kamimura and Honma, 1963; Kamimura, 1966: 767, Figure 10). If we interpret the change of average size along the equator as a reflection of migration, then a modification of effort allocation along the equator would tend to modify recruitment size. It is implicit, however, that the utility of controlling recruitment size of yellowfin tuna by closing or partially closing certain areas to fishing depends on the assumption that there is a single population of yellowfin tuna in the equatorial Pacific Ocean. That this is unlikely, in general, was shown by Joseph, Alverson, Fink, and Davidoff (1964); they provided evidence that the yellowfin tuna harvested in the near-coastal eastern tropical Pacific fishery constitute a subpopulation that is distinct from the yellowfin tuna harvested in the rest of the equatorial Pacific. Furthermore, the yellowfin tuna of the central and western Pacific may comprise more than one subpopulation. Evidence for this possibility includes (1) trends in morphometric measurements of yellowfin tuna along the equator (Royce, 1964), (2) the size gradient along the equator, and (3) the common occurrence of small yellowfin tuna in the vicinity of all the islands in the equatorial western and central Pacific Ocean. First, Royce's data could be interpreted as being generated by a series of discrete populations. Second, the average sizes presented by Murphy and Shomura (1955) can also be interpreted as being generated by two or three discrete populations (of lengths): one population between long. 140° and 170° E. with an average length of about 120 centimeters; a second population between long. 180° and 150° W. with an average length of about 140 centimeters; and a third population between long. 150° and 120° W. with an average length of about 150 centimeters. These populations of lengths might reflect the existence of discrete yellowfin tuna subpopulations along the equator. Third, the common occurrence of small yellowfin tuna—all of about the same size—in the insular waters of the many islands in the western and central equatorial Pacific suggests that not all of the yellowfin tuna along the equator are migratory. Although these points do not disprove the migration hypothesis, they do indicate the possibility of alternate interpretations, one of which is that there are several discrete populations or subpopulations of yellowfin tuna along the equator; if so yield-per-recruit studies should be made on each. A yield-per-recruit study based on the assumption that there is a single population, when in fact there are several subpopulations, might result in recommendations which would severely under- or over-fish some of the subpopulations. Therefore, suggestions for increasing the yield-per-recruit along the equator by manipulating size at recruitment would depend on the population structure of this region. If the size distribution along the equator is primarily produced by phenomena associated with migration, then yield-per-recruit might be increased by allocating different amounts of fishing effort to different locations along the migratory route. If a lower recruitment size is desired, more effort would be allocated in the Trust Territory area; if a higher recruitment size is desired, more effort should be allocated in the Christmas Island area. By contrast, if the size distribution along the equator reflects the existence of discrete subpopulations, each with different vital statistics, then each subpopulation should, for maximum efficiency, be managed as a distinct entity. Since the size of yellowfin tuna tends to be related to distance from islands (Shomura and Murphy, 1955), this approach would probably involve a policy that would partition effort between insular and oceanic regions.

We have so far restricted our discussion of manipulating the size of recruitment of yellowfin tuna to the use of only longline gear, and to the modification of the location of fishing (rather than the selectivity of the gear), without changing fishing intensity. We do not know to what extent the selectivity of the longline gear itself could be modified. Rothschild and Nakamura (MS) found that rather large differences in bait size had no effect on the catch rate or average size of yellowfin tuna caught.

Thus, if we restrict ourselves to longline gear we may not be able to alter recruitment size—by modifying the selectivity of the gear itself or by altering fishing location—over a sufficient range to affect significantly the yield-per-recruit relation. We might then shift (if size at recruit-

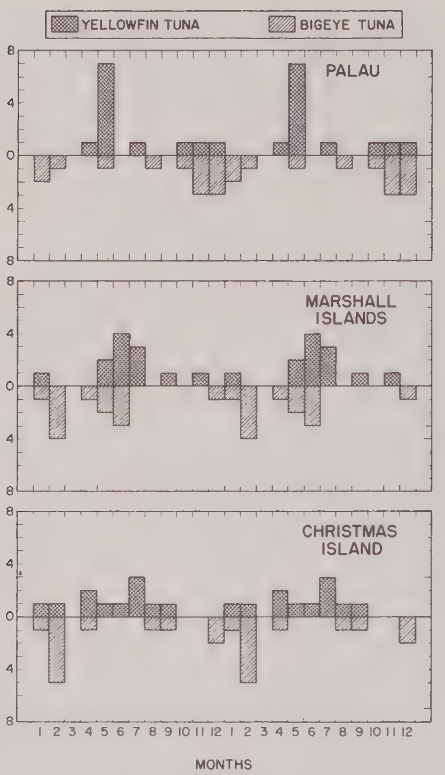


Figure 15.—Frequency distribution of months of maximum CPUE (100 hooks) for each year, 1953-65, for yellowfin and bigeye tuna in the Palau, Marshall Islands, and Christmas Island quadrangles. The month scale is plotted twice to avoid partitioning midwinter peaks.

ment were the only consideration) to surface fishing with pole and line, a method by which considerably smaller yellowfin tuna can be taken than by longline. In this respect it is interesting and also somewhat curious that the eastern Pacific Ocean coastal fishery for yellowfin tuna occupies a much smaller area than that occupied by the longline fishery, but produces about 90,000 metric tons of yellowfin tuna by surface fishing gear.

Many schemes could be devised for increasing the efficiency of capture of yellowfin tuna, but investigating the practicality of any such scheme on a commercial scale is likely to be expensive and difficult. One possiblity, however, might be considered: This involves determining an optimal fishing strategy with respect to the path a fishing boat takes among the fishing areas. In determining this path, advantage would be taken of the information contained in the periodicities in apparent abundance of yellowfin tuna (and other species) at various points in space and time. As an example of these periodicities we have plotted the average catch per 100 hooks for yellowfin and bigeye tuna for 1953-65 for three 10° quadrangles of ocean along the equator—the Palau, Marshall Islands, and Christmas Island quadrangles. We then compiled the frequency distribution by months of the maximum CPUE for yellowfin and bigeye tuna (Figure 15). The CPUE for yellowfin tuna tends to exhibit maxima in May-August and in midwinter; the major spring-summer peak tends to occur progressively later in the year, from west to east. This information on periodicity could be related to expected catch and the cost of fishing in each quadrangle, to develop a mathematically programmed optimum fishing route for yellowfin tuna.

We conclude this section on yellowfin tuna by indicating the location of fairly recent high apparent abundance indices and the regions of highest catches. In recent years areas of high apparent abundance (1) tended to be concentrated in the equatorial western Pacific, (2) tended to be most confined in distribution during the first quarter of the year, and (3) extended farthest east in the second or third quarters of the year, and in some quarters extended to the approximate longitude of the Hawaiian Islands—as in most of 1962 and the second and third quarters of 1964 and 1965 (Figure 16). In contrast to the distribution of apparent abundance, the distribution of catches ranged nearly to the coasts of the Americas (Figure 17). Thus, although areas of high apparent abundance tended to be restricted to the western Pacific (some as far east as the vicinity of the Hawaiian Islands), relatively large catches were made over a much wider area of presumably lower catch rates.

Bigeye Tuna

As indicated previously, CPUE and average size of bigeye tuna declined as the intensity of Japanese longline fishing increased. Whereas the catches of the other species of tunas reached nearly constant values in the mid-1950's, the catches of bigeye tuna continued to increase until the early 1960's. This increase was related to the eastward expansion of the fishery into the virtually unfished areas of the eastern Pacific—which are characterized by a higher apparent abundance of bigeye tuna than other regions of the Pacific. In the early 1960's, however, the Japanese longline effort extended to the shores of the Americas, and declines in CPUE and average size for bigeye tuna (see Suda and Schaefer, 1965; Kume and Schaefer, 1966; and Kume and Joseph, 1966) were accompanied by a stabilization of catches at about 100,000 metric tons per year. Thus, like the yellowfin tuna, the bigeye tuna exhibited declines in CPUE and average size, and a stabilization of total catch. These circumstances suggest that substantial increases in the catch of bigeye tuna are unlikely (with the present distribution of effort, intensty of effort, and gear selectivity). This conclusion tends to be corroborated by the studies reviewed by Kamimura (1966). In these studies the coefficient of instantaneous natural mortality was estimated to be 0.4. The estimated coefficient of instantaneous fishing mortality was 0.3 in 1958-60, 0.35 in 1961, 0.45 in 1962, and 0.67-0.70 in 1963. On the basis of these mortality coefficients Kamimura presented values—on a stock-and-recruitment rather than a steady-state model—of maximum sustained yield of bigeye tuna of about 110,000 tons. The maximum sustained yield would have been attained at a level of fishing ($F = 0.50$) that was slightly greater than the effort expended in 1962. Silliman (1966), on the other hand, estimated that the MSY is lower (78,000 metric tons per year) at a fishing intensity corresponding to $F = 0.65$. Using the estimates presented by Kamimura, we have plotted the eumetric fishing line for bigeye tuna based on a steady recruitment. On the basis of this line it appears that both estimates of maximum sustained yield result in about the same recruitment size. Kamimura's estimates indicate that present fishing is nearly eumetric. The eastern Pacific bigeye tuna size distributions presented by Kume and Joseph (1966) suggest, however, that recruitment occurs at about 90 centimeters in length (incidentally Yukinawa (1958) showed on the basis of much smaller samples a recruitment length of about 120 centimeters for the eastern Pacific). Now it is clear that the largest recruitment sizes for bigeye tuna occur in the eastern Pacific, so an average recruitment size for this species for the entire Pacific Ocean must be somewhat less than 90 centimeters. This relation, places the optimum fishing level at an F of about 0.3 or at the 1958-60 level of fishing. We cannot, at this point, indicate which is the better alternative, especially in view of some of the complex problems of estimating an F that is an average of F values that vary spatially and temporally. We simply use this as an example to demonstrate that with imperfect information several alternative solutions are possible.

Perhaps the best way of modifying the yield-per-recruit of bigeye tuna would be to modify recruitment size for a fixed fishing intensity. Recruitment size could also be modified by allocating effort with respect to the size distribution or by modifying the selectivity of the longline gear. The size distribution of bigeye tuna is such that fish less than 80 centimeters long are taken in relatively small numbers at the surface in the eastern Pacific Ocean (Alverson and Peterson, 1963), in the Japanese pole-and-line fishery for albacore and skipjack tuna in the Northwest Pacific Ocean (Honma and Kamimura, 1955), and occasionally in Hawaiian waters; bigeye tuna taken on the North Pacific longline grounds tend to be about 80 to 120 centimeters long (Kamimura and Honma, 1953); and most of those taken on the equatorial grounds are longer than about 120 centimeters (Yukinawa, 1958; Kume and Joseph, 1966). In addition, bigeye tuna on the equatorial grounds exhibit a trend toward increasing size from west to east, which is similar to that exhibited by yellowfin tuna. Thus, the average size at recruitment and the average size in the catch can be controlled to some extent by an allocation of the spatial distribution of effort. As indicated previously, it is not known to what extent modifications of the longline gear alter longline selectivity. Fishing with pole-and-line surface gear would, for example, result in a considerable reduction in the average size of the bigeye tuna caught. On the other hand the vulnerability to surface fishing is probably several orders of magnitude less for small bigeye tuna than for yellowfin tuna.

The eumetric curve and the relatively high fishing intensity that is now being exerted on the bigeye tuna suggest that a curtailment of fishing on the northern longline grounds would result in an increased average recruitment size and consequently a greater yield-per-recruit. This, of course, would depend on whether the bigeye tuna taken on the North Pacific grounds and those taken on the equatorial grounds are drawn from a common population. We cannot be certain of this homogeneity, but observe that the bigeye tuna taken on the northern grounds are essentially immature fish and that spawning is negligible in the North Pacific bigeye tuna area. It is likely that the spawning area is in equatorial waters, as shown by the relatively large numbers of tuna larvae in these waters and the studies of Kikawa (1962) that showed that the gonads of bigeye tuna in equatorial waters are in an advanced state of maturity. At least some of these bigeye tuna spawned in equatorial waters are recruited into the North Pacific longline grounds before being recruited into the equatorial fishery. Whether the bigeye tuna constitute a homogeneous population in the equatorial area is not clear. They exhibit the same type of size gradient as the yellowfin tuna, but the young stages are not commonly observed in equatorial waters. Furthermore, there have been no detailed analyses of morphometric measurements of bigeye tuna as have been available for the yellowfin tuna.

The efficiency of longline fishing for bigeye tuna might also be increased if the fishing vessels could be programmed to fish on an optimal path. That this may be possible is indicated in Figure 15, which shows that fishing for bigeye tuna generally is best during midwinter and perhaps peaks a few months earlier in Palau than in either the Marshall Islands or at Christmas Island. It is obvious, however, that the expected CPUE for bigeye tuna would not be as high in any of these quadrangles as in many quadrangles in the eastern Pacific. At the same time, however, it might be economically advantageous to fish one of these quadrangles of lesser apparent abundance in the central or western Pacific. This strategy would be based not only on expected catch of bigeye tuna, but also on expected catch of other species, the value of each species, and the cost of fishing in terms of distance and the probability of obtaining a greater profit in some other area.

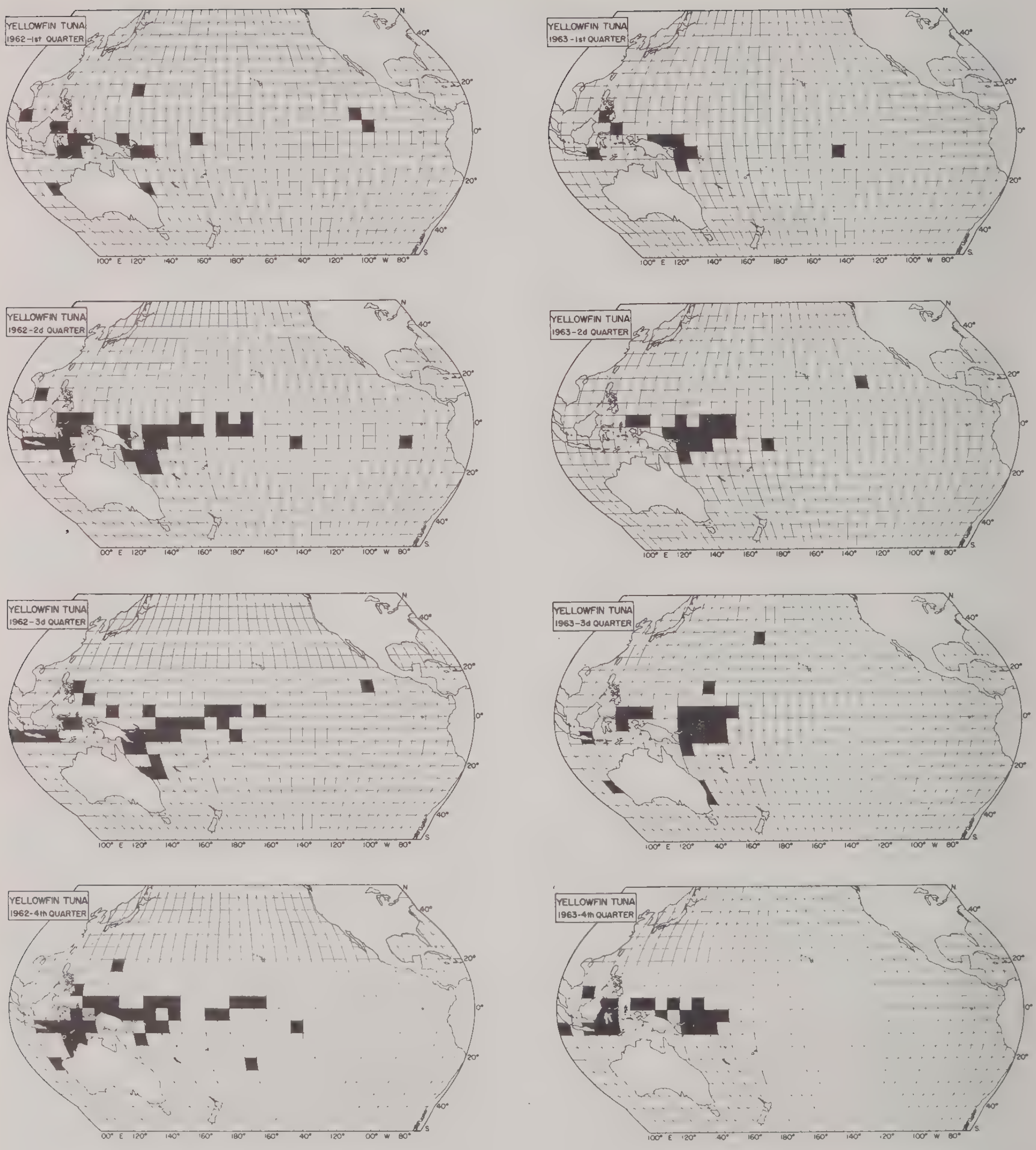
The location of greatest apparent abundance of bigeye tuna now tends to be northeast of Hawaii and roughly on a line between Hawaii and Ecuador (Figure 18). The density of high apparent abundance of bigeye tuna appears to have decreased steadily since 1962 with the first quarter of the year generally exhibiting the highest apparent abundance. This is noticed particularly in 1964 and 1965 when there was a considerable decline in the regions of high apparent abundance.

The locations of high catches are roughly similar to the regions of high apparent abundance (Figure 19); although the region of high catches tends to extend farther west than the region of high apparent abundance. Relatively large catches were made on the northern grounds only in 1963. It is interesting to compare the number of 5° quadrangles in the equatorial grounds with catches greater than 10,000 fish with the dynamics of CPUE. The number of 5° quadrangles in the equatorial region with catches greater than 10,000 fish was 56 in 1962, 78 in 1963, 52 in 1964, and 32 in 1965. Thus, according to Figures 18 and 19, CPUE tended to be relatively high in 1962 and catch was relatively low, CPUE declined in 1963 and catch increased, CPUE declined further in 1964 and catch declined, and CPUE tended to be low in 1965 and catch dropped considerably. The declines in CPUE tend to move the apparent abundance to the east while at the same time moving catch to the west. It is also clear that the Japanese longline fishery has been a causative agent in reducing the catch of bigeye tuna by the Hawaiian fleet (see Hida, 1966: Figure 1).

Thus, as with the yellowfin tuna, it appears that the opportunity for increased catches of bigeye tuna are limited.

Albacore

As we have noted previously, the albacore comprise a North Pacific and a South Pacific population. In the North


YELLOWFIN TUNA 1962-1st QUARTER
YELLOWFIN TUNA 1963-1st QUARTER
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YELLOWFIN TUNA 1962-4th QUARTER
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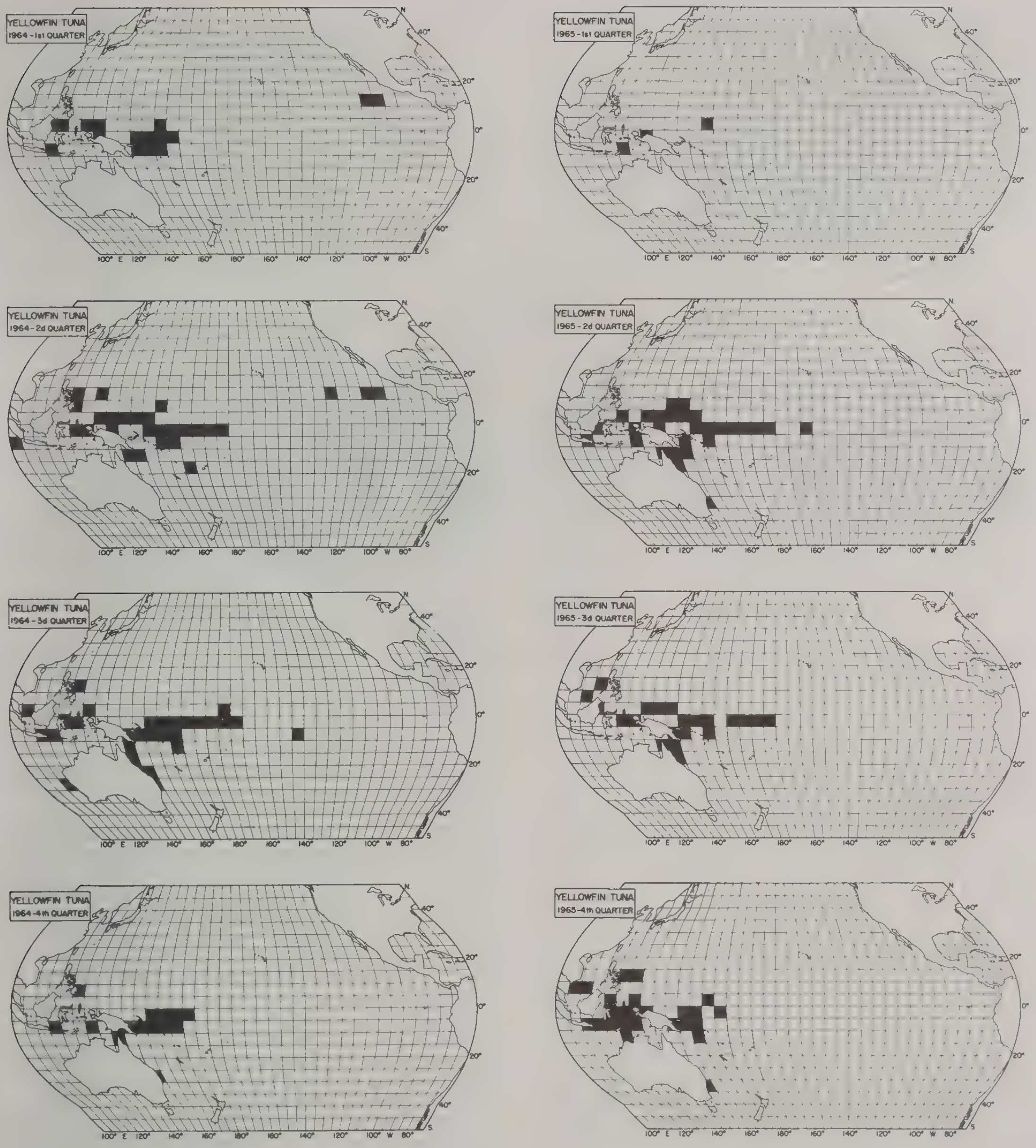
Figure 16.—Shaded areas show 5° quadrangles of the Pacific Ocean for each quarter of the year (1962 to 1965) where yellowfin tuna CPUE exceeded 2.5 fish per 100 hooks (compiled from ARJTF).


YELLOWFIN TUNA
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YELLOWFIN TUNA
1965 - 1st QUARTER
YELLOWFIN TUNA
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YELLOWFIN TUNA
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Figure 16.—Continued

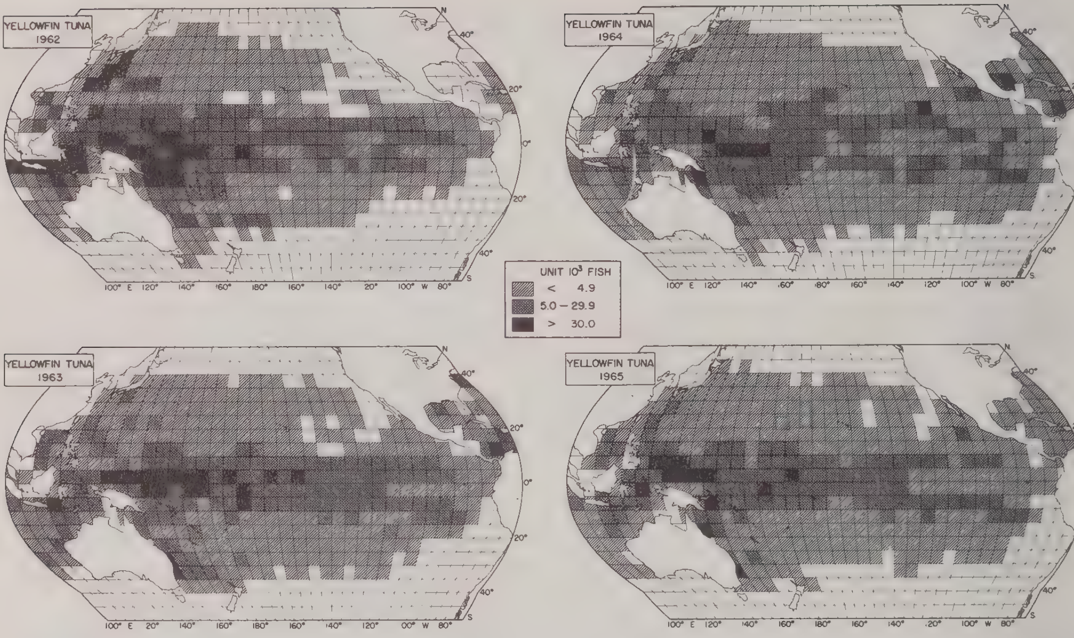

Figure 17.—Estimates of catch of yellowfin tuna by the Japanese longline fleet by 5° quadrangles from 1962 to 1965 (compiled from ARJTF).

Pacific the albacore was the first species of fish to be intensively exploited by the Japanese longline fishery. The fishery exhibited rather large declines in apparent abundance just after World War II and the catch remained level at about 20,000 metric tons per year. Larger catches of albacore from the North Pacific grounds appear unlikely.

The most extensive studies of the albacore taken on the North Pacific albacore longline grounds have been conducted by Akira Suda (e.g., 1959). His work was summarized by Kamimura (1966). Suda interpreted the decline in apparent abundance of albacore as having occurred primarily in the early 1950's. In the mid-1950's CPUE and catch both leveled off. Any fluctuations in apparent abundance were related to fluctuation in recruitment. Estimates of natural mortality and fishing mortality were made on the basis of the interpretation that there was an initial rapid decline in CPUE followed by an equilibrium. The equilibrium values were $F = 0.2$ and $M = 0.2$; these values had been maintained since 1955. A yield isopleth was presented which indicated that the albacore on the North Pacific longline grounds are being underfished with respect to maximum sustained yield.

As we understand the summary in Kamimura, an increase in fishing intensity would decrease the CPUE and the recommendations for future fishing involve a general strategy of continued underfishing. Studies by Rothschild and Yong (MSa) seemed to indicate that the albacore on the North Pacific longline grounds tend to be overfished rather than underfished. We are continuing to study this problem.

The question of optimal yield-per-recruit for albacore in the North Pacific Ocean is to some extent more complicated than the same question for either the yellowfin or bigeye tuna, because the single population of albacore in the North Pacific is exploited in substantial quantities by three fisheries: the North American coastal fishery, the Japanese winter longline fishery, and the Japanese spring livebait fishery. Suda's suggestion (in Kamimura, 1966) that a more rational exploitation of albacore would obtain if this species could be harvested at a smaller size implies that an intensification of the North American coastal fishery for albacore would tend to increase the yield-per-recruit.

The albacore in the South Pacific Ocean, as pointed out previously, have been harvested in relatively large quantities since 1956. Detailed studies of the yield potential of the albacore have not been made. Otsu (1966) showed a decline in apparent abundance since 1960.

Recent trends in albacore catch and apparent abundance can be seen in Figure 20 and Figure 21. As is well known, the peak apparent abundance of albacore occurs during the first quarter in the North Pacific fishery. The South Pacific fishery is much more extensive in both time and space, and the catches extend over a much wider area than the region of relatively high CPUE. Landings are larger and are distributed over a much more extensive area in the southern fishery than in the northern fishery.

It appears that the South Pacific albacore fishery may be reaching its maximal catch: The CPUE has been exhibiting a decreasing rate of increase (and may be very close to decreasing), average size is declining, the total catch has stabilized, and the distribution of fishing is extensive.

Skipjack Tuna

As indicated earlier the largest catches of skipjack tuna are made in the coastal waters of the Americas and Japan (Table 1).

Despite the large catches the apparent abundance of skipjack tuna has not been affected in either the American or the Japanese fisheries (Broadhead and Barrett, 1964; Kawasaki, 1965, Part I). A variety of models has been proposed to explain the movements and migrations of skipjack tuna (e.g., Kawasaki, 1964). Rothschild (1965) proposed a model based on various evidence which postulated that the skipjack tuna that are exploited in the eastern Pacific coastal fishery spawn west of about long. 130° W. The young fish move into the eastern Pacific fishing area at an age of about 1 year. These fish constitute an adolescent stock which is exploited on a northern ground, mostly off Baja California, and a southern ground, which extends from Central America south to the Peru-Chile border. After remaining in the eastern Pacific fisheries, where they are exposed to fishing mortality, for several months, the remaining fish, with the onset of sexual maturity escape into the central Pacific spawning area. (The movement pattern is diagrammed in Figure 22). The evidence for this pattern has been summarized by Sette and Rothschild (1966) as follows:

1. The effect of the California fleet's fishery on the abundance of this stock is so slight as to be undetectable by conventional population-dynamics analysis.
2. The fishery in the eastern Pacific takes very few fish old enough to be even approaching maturity.
3. Plankton tows in the eastern Pacific take few larvae . . . in relation to the numbers of fish of commercial size caught there.
4. Skipjack tuna larvae are taken much more commonly in plankton tows in tropical and subtropical waters to the westward in the broad band across the central Pacific.
5. Three skipjack tuna, small when tagged in the eastern fishery, were recaptured in the central Pacific—two in Hawaii after 21 and 28 months, respectively, and one in the Line Islands area after 16 months. All were much larger than when tagged. Of interest in this context is an immunogenetic determination that skipjack tuna in a small sample from the eastern Pacific fishery were indistinguishable from one of the two subpopulations in the Hawaiian fishery, identified with the same reagents.
6. Skipjack tuna much larger than those commonly caught in the eastern Pacific furnish the bulk of the summer catch in Hawaii, where they are called "season fish."
7. Large skipjack tuna are frequently taken incidentally on longlines in a broad band across the tropical and subtropical Pacific.

These items taken together are strongly suggestive, but not conclusive, evidence that considerable numbers of the skipjack tuna supporting the eastern Pacific fishery are members of a subpopulation that ranges far from the fishing area in later life.

Although there is a reasonable certainty that skipjack tuna circulate between the eastern Pacific coastal fishery and the central Pacific Ocean in the manner described, the destination of the maturing fish in the central Pacific is not immediately clear. In this respect it is also reasonably certain that the skipjack tuna of the central Pacific Ocean comprise at least two subpopulations. This conclusion is based on temporal-spatial isolation between the skipjack tuna that spawn in the Hawaii region in the northern summer and those that spawn in the Marquesas-Tuamotu region in the northern winter. Temporal-spatial isolation at spawning has been described in many organisms as a basis for infra-specific differentiation (see for example Mayr, 1963). That this temporal-spatial isolation in skipjack tuna reflects differentiation at the subpopulation level (Mayr might call each subpopulation a sibling species) has been suggested by immunogenetics studies reported by Fujino (1967).

The existence of at least two subpopulations of skipjack tuna in the central Pacific Ocean has profound implications with respect to the resource potential of the species in the central and eastern Pacific Ocean. For example, Rothschild (1965) speculated for a variety of rather weak reasons that the skipjack tuna of the Marquesas-Tuamotu area do not circulate through the eastern Pacific fishery. If this speculation is true the undoubtedly huge skipjack resource of the Marquesas-Tuamotu area is virtually unexploited.

The hypothesis concerning the circulation of skipjack tuna through the eastern Pacific as depicted in Figure 22 enables the formulation of a model by which yield estimates can be made. This model involves computing estimates of the yield-per-recruit under the present partial-life exploitation of skipjack tuna in the eastern Pacific. Estimates of yield-per-recruit are also computed under the hypothetical circumstance of the skipjack tuna being exploited in the eastern Pacific and after it escaped the eastern Pacific. The ratio between the yield-per-recruit under whole-life exploitation to yield-per-recruit under partial-life expectation provides an estimate of the extent to which yield could be increased by changing the exploitation regime. Preliminary estimates by Rothschild (1966b) showed that changing the exploitation regime from harvesting skipjack tuna only in the eastern Pacific to harvesting in the eastern Pacific and in the central Pacific would result in increases in yield that are of an order of 100,000's of tons. Independent estimates by Silliman (1966) were of this same order of magnitude. One unit of 100,000 tons of skipjack has a value of $25 million to the fishermen, $62.5 million to the producer, and $100 million at the retail level.

It is reasonable to assume that the skipjack tuna taken by the Japanese fishery circulate through the Japanese coastal fishery in the same manner as skipjack tuna circulate through the eastern Pacific fishery because (1) the skipjack tuna harvested in the Japanese coastal fishery are, like those harvested in the eastern Pacific, small adolescent fish and (2) the amount of spawning off the coast of Japan appears to be negligible. Kawasaki (1965 and earlier papers) indicated that skipjack tuna probably move into the coastal waters of the Japanese archipelago via the Ryukyus and Izu-Bonin chains. It is likely that the skipjack tuna that enter the Japanese fishery have been spawned as far south as the Trust Territory. The reason for indicating the similarity in the dynamical structure of the skipjack tuna taken in the Japanese coastal fishery is that the same escapement-yield relation is likely to apply to the Japanese escapement as applied to the eastern Pacific escapement. Thus, we could expect that escapement from the Japanese fishery might provide yields of 100,000's of tons in the central Pacific Ocean.

Skipjack tuna harvested in the eastern Pacific fishery and the Japanese fishery thus spend a good part of their life in

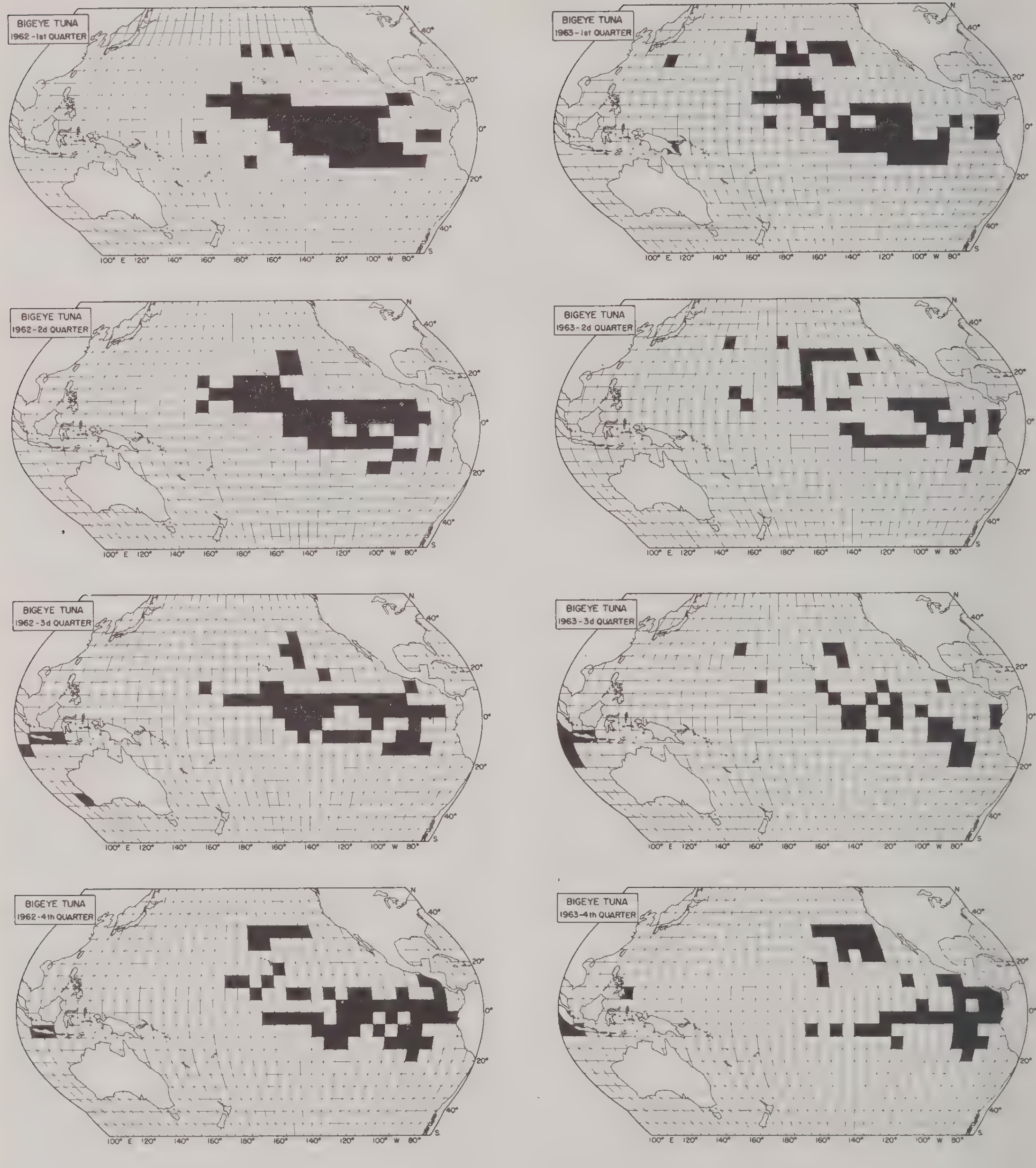
BIGEYE TUNA
1962-1st QUARTER
BIGEYE TUNA
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Figure 18.—Shaded areas show 5° quadrangles of the Pacific Ocean for each quarter of the year (1962 to 1965) where CPUE of bigeye tuna exceeded 1.5 fish per 100 hooks (compiled from ARJTF).

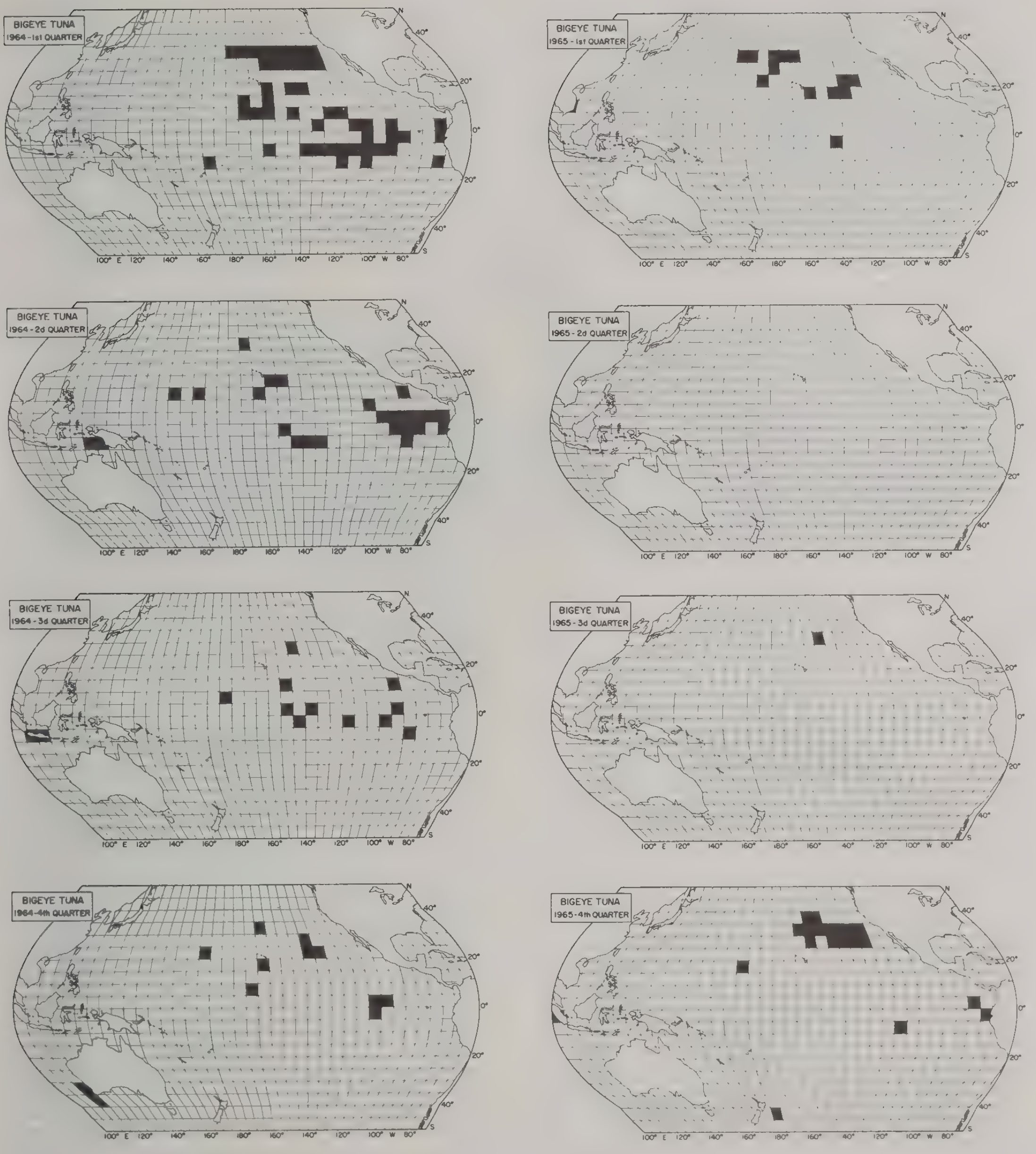
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Figure 18.—Continued

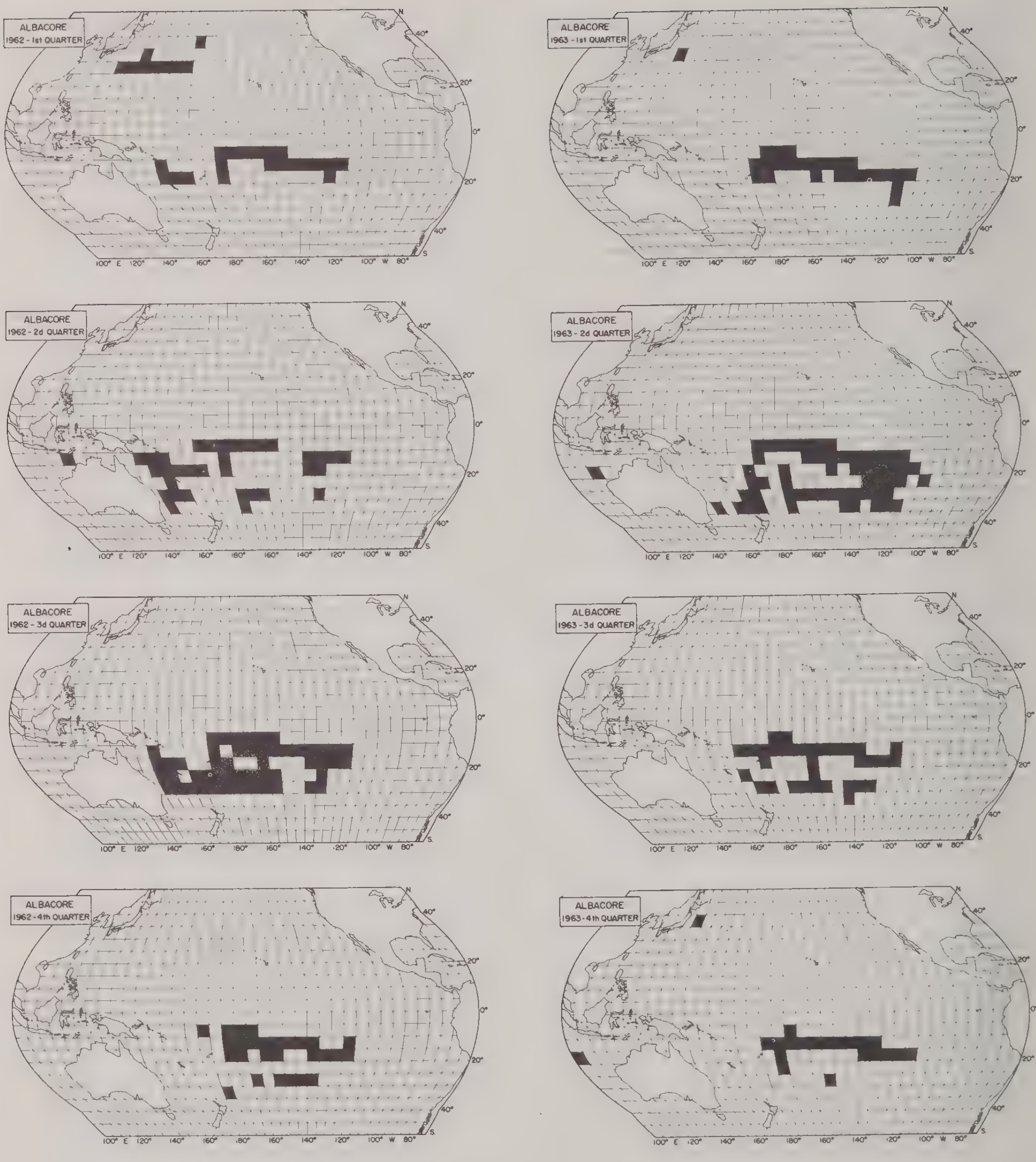
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Figure 20.—Five-degree quadrangles of the Pacific Ocean for each quarter of the year from 1962 to 1965 outlining the areas where CPUE for albacore exceeded 1.5 fish per 100 hooks (compiled from ARJTF).

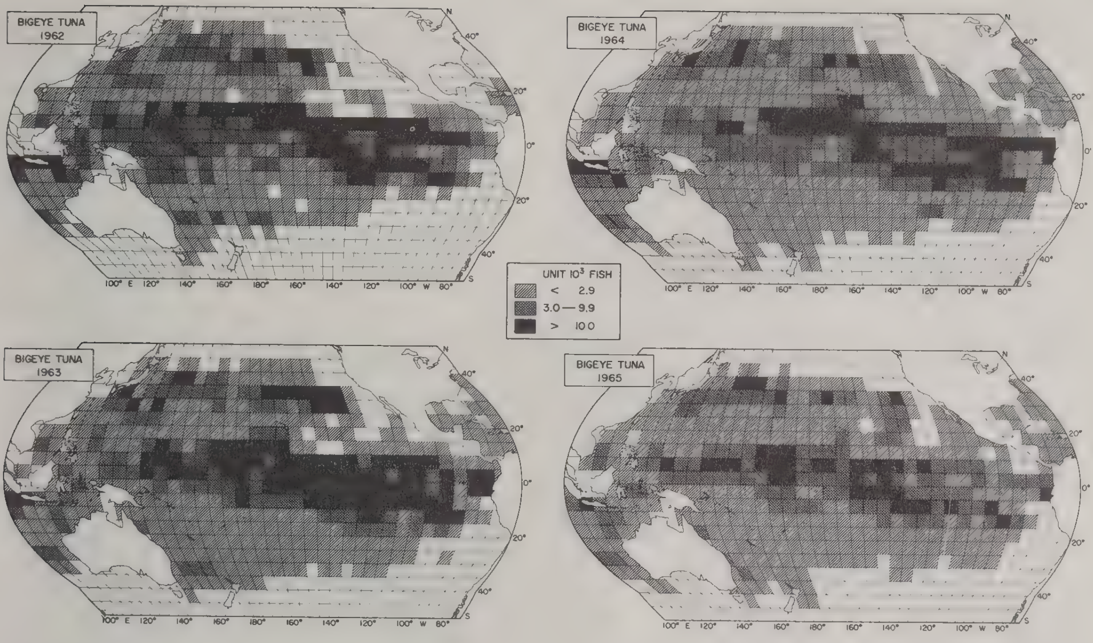

Figure 19.—Estimates of catch of bigeye tuna by the Japanese longline fleet by 5° quadrangles from 1962 to 1965.

the central Pacific. Other sources of skipjack tuna in the central Pacific include the fish which apparently never enter the existing coastal fishery areas. Skipjack tuna are commonly taken in the central Pacific fishery at the same time and at the same size as in the coastal fisheries. Major fisheries for skipjack tuna occur at the cold water-warm water interfaces at three "corners" of the tropical ocean: off Baja California, off northern South America, and off northern Japan. Is there a similar harvestable stock off New Zealand or Australia?

We can conclude from the observations given in this paper and the frequently made observation that there are no observable effects of fishing on the established fisheries in Hawaii, Japan, or the coasts of the Americas that there is a sizable potential of yields of skipjack tuna in the central Pacific and that these yields are of the order of 100,000's of metric tons.

The important question concerning the skipjack tuna resource is to translate the biomass into a maximum-sustained, profitably harvested yield. To be profitably harvested skipjack tuna must occur at catchable densities high enough to return to the fishermen the expense of reaching them.

The expense of reaching areas of high densities of fish (making the reasonable assumption that the fish are not uniformly distributed) is a function of, among other things, the type of gear. As indicated earlier, surface fishing with live bait is likely to be expensive, especially in areas where live bait is scarce. The expense arises from two factors: the cost involved in fishing for bait (Hawaiian skipjack tuna fishermen spend about 30-40 percent of their time fishing for bait when they could be fishing for skipjack tuna) and the expense of fishing for schools that do not "bite." As indicated previously about 50 percent of the skipjack tuna schools fished in the Hawaii fishery do not bite. As mentioned earlier, for skipjack tuna to be landed under the present fishing system in the central Pacific, the fish school must be at or near the surface; birds must be present and react positively to the school; the fishermen must be in the vicinity of the birds and the school, and must sight the birds; and finally the skipjack tuna must bite.

Naturally, the first thought that comes to mind in eliminating the bait problem and the necessity for the fish to bite is to use an alternative type of gear that requires neither live bait nor fish to bite. The purse seine is such a gear. Purse seines were experimentally used in the central Pacific in the early 1950's but they were not as technologically advanced as those available today; they met with little success (Murphy and Niska, 1953). Among the reasons given for the unsuccessful trials were that the schools were small and fast moving and that the deep thermocline enabled them to sound beneath the net. It is possible that greater success might be attained with the new fast-sinking nets and a power block. It should also be noted that, although the thermocline in much of the central Pacific is deep, it is shallow in some areas, as in the center of some of the eddies that are generated in the wake of the Hawaiian Islands. Therefore, although purse seining as it is accomplished in the eastern tropical Pacific may not be suitable for the central Pacific, nets and boats that are differently designed might be highly efficient. The follow-

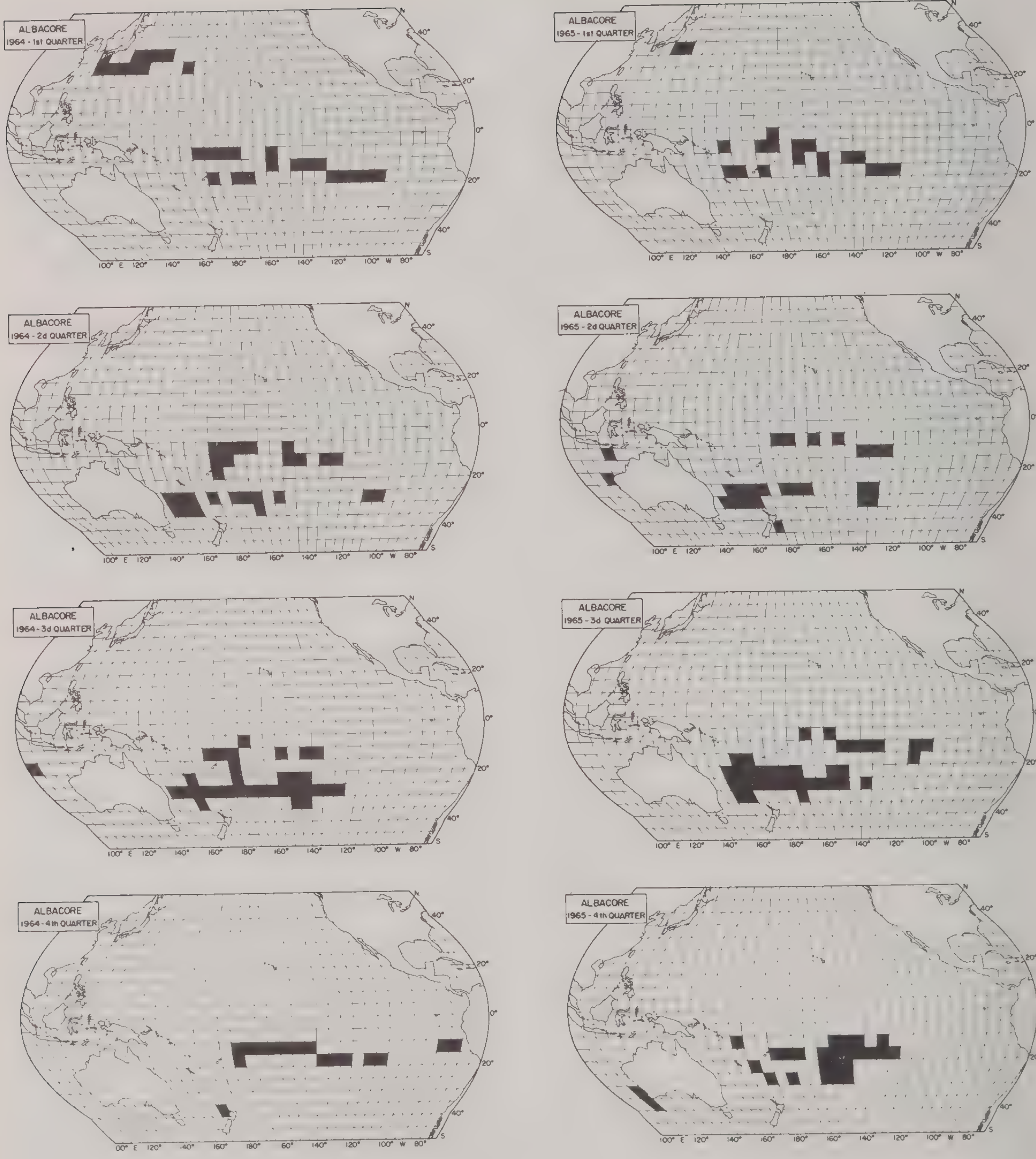
ALBACORE 1964 - 1st QUARTER
ALBACORE 1965 - 1st QUARTER
ALBACORE 1964 - 2d QUARTER
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Figure 20.—Continued

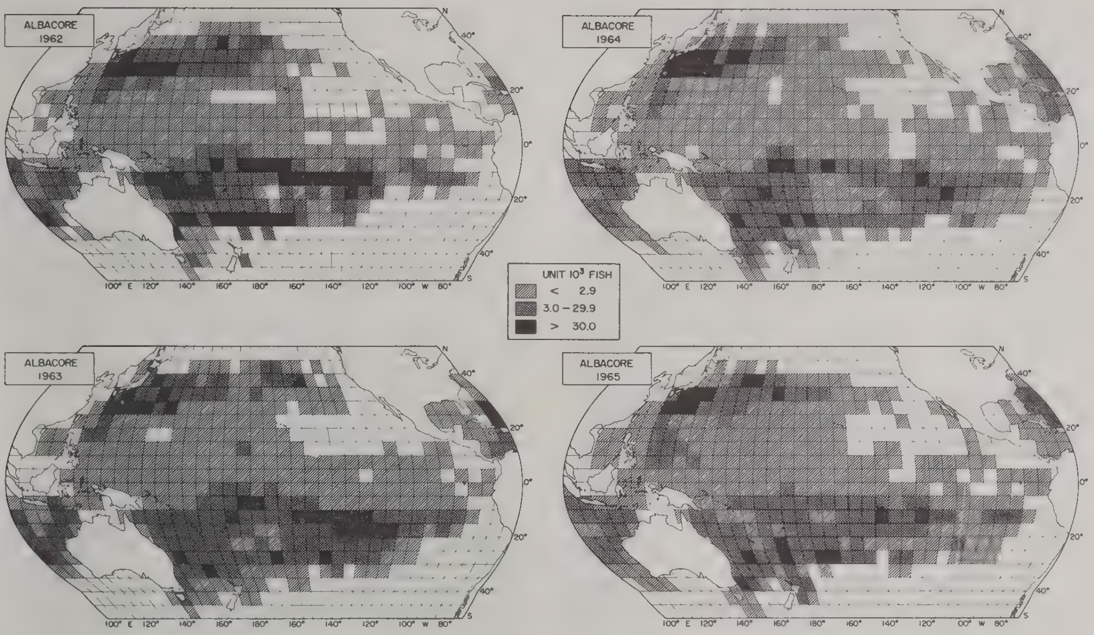
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Figure 21.—Estimates of catch of albacore by the Japanese longline fleet by 5° quadrangles from 1962 to 1965.

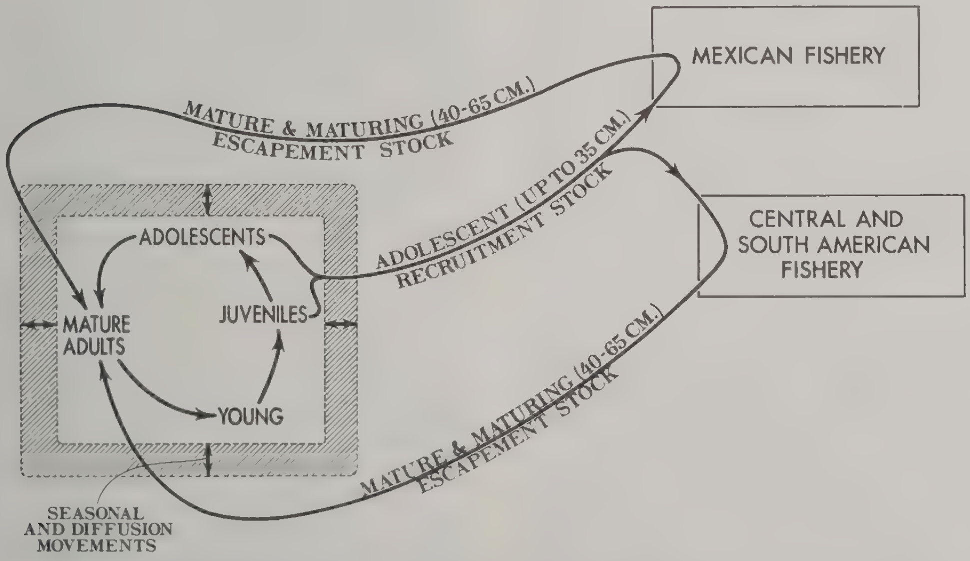
MEXICAN FISHERY
CENTRAL AND SOUTH AMERICAN FISHERY
MATURE & MATURING (40-65 CM.) ESCAPEMENT STOCK
ADOLESCENT (UP TO 35 CM.) RECRUITMENT STOCK
MATURE & MATURING (40-65 CM.) ESCAPEMENT STOCK
ADOLESCENTS
JUVENILES
MATURE ADULTS
YOUNG
SEASONAL AND DIFFUSION MOVEMENTS

Figure 22.—Diagram showing the movement of skipjack tuna between the central Pacific and the Mexican and South American fisheries of the eastern Pacific (taken from Rothschild, 1965).

ing quotation from the *Shin Suisan Shimbun,* December 4, 1967, might augur the use of purse seines in the central Pacific Ocean:

> The Kinkai Hogei Whaling Company's purse seiner, *Nissho Maru* (253 gross tons), which departed Japan on November 10, 1967 for the South Pacific, found excellent fishing off New Guinea between 7° N.-8° N. latitudes. The vessel, which began fishing about November 22, landed close to 70 metric tons of yellowfin (44- to 66-pound fish) and skipjack as of November 28 and was expected to fill her holds in one more set. A carrier was sent to take the vessel's catch. This operation has drawn much attention in Japan, since two years ago another Japanese seiner fished in the same area with disappointing results. The recent success is attributed to the use of a new kind of purse seine developed jointly by Taito Seimo Net Manufacturing Company and the Tokai Regional Fisheries Research Laboratory at a cost of $22,222. In view of the rapid flow of the current and deep thermocline in the western equatorial Pacific, the net was built with a larger mesh in the upper section to reduce resistance to the current flow and designed for faster sinking to prevent the escape of fish from under the net during setting.

Thus, the skipjack tuna has an exploitation status that is different from the other commercially exploited tunas of the pelagic high-sea areas of the Pacific Ocean. Despite the landing of over 200,000 tons of skipjack tuna each year, there is no evidence in the literature that fishing has had any effect on the stocks. Albacore and yellowfin and bigeye tuna all show the effects of exploitation and are probably being harvested at their maximum capacity. The yield potential of the skipjack tuna from the noncoastal regions of the Pacific Ocean is, however, estimated to be of the order of 100,000's of tons.

One of the questions that arises concerns the harvesting regime that will enable maximum sustained catches of skipjack tuna. Since the size at recruitment in the coastal fisheries is uncontrollable, fishing intensity would have to be adjusted to correspond with a maximum sustained yield. The fishing intensity which would give a maximum yield might not result in as high a yield if recruitment size could also be adjusted. In fact it is improbable that the best recruitment size is that at which the fish presently enter the fishery. This adjustment could easily be effected if fishing could be accomplished outside the present fishing area. The practicality of fishing outside the present near-coastal fishing area is an open question. It is a question that may not, however, be answered without a more sophisticated fishing technology than that which is now available.

CONSTRAINTS ON THE FULL UTILIZATION OF THE PELAGIC RESOURCES OF THE PACIFIC OCEAN

The pelagic resources of the Pacific Ocean can be categorized into major groups. First, there are resources that are currently utilized. Some of these, such as the yellowfin tuna, the bigeye tuna, the albacore, and some of the billfishes, are probably being harvested at near-peak levels with existing gear and fishing methods. Others, such as the skipjack tuna, are considerably underutilized. For the tunas we have attempted to outline what is known of their dynamics, their potential harvest, their temporal-spatial distribution, and some fishery-oriented aspects of their life history. We have not, however, considered the billfishes or essentially unharvested resources such as the squids. These unharvested resources represent a tremendous variety of organisms and constitute a very large biomass.

Our paper on Pacific oceanic fish resources, therefore, has been somewhat parochial because of our emphasis on the tunas. The emphasis on the tunas is the result of the considerable body of information which is published on this group relative to other groups, and the likelihood that the tunas—the skipjack tuna in particular—represent a considerable harvestable potential for which there is an extant industrial demand. In several areas skipjack tuna occur in commercial concentrations, have a high unit value, and can be captured with existing harvesting technology. On the other hand, we should be careful not to place an inordinate amount of weight on the tunas because they probably constitute a relatively small proportion of the biomass of the pelagic areas of the tropical and subtropical Pacific Ocean.

What are the constraints on harvesting the skipjack tuna and the large biomass of little known or innominate pelagic species of the Pacific Ocean? The constraints mostly involve our ignorance or uncertainty about (1) the species that are at present unharvested, but could be harvested at a profit, (2) the potentials of underexploited species, and (3) the economically more efficient ways of fishing both the heavily exploited and the underexploited species. The extent of these uncertainties can be equated with the risk of investment in a fishing operation. Judging by the limited growth of the U.S. fishing industry, this problem of investor uncertainty is common to many of our aquatic resources. This problem would be alleviated by (1) identifying species capable of sustaining increased harvests, (2) developing sophisticated harvesting gear that would result in manifold increases in efficiency and corresponding decreases in the cost of fishing, and (3) developing new markets and uses for fishery products. This information would constitute a prospectus for the investor; it would indicate those areas of the fishing industry where investment could yield higher returns at a lower relative risk than in other industries. The preparation of a prospectus is an expensive undertaking. In general the resource must be identified and mapped in both time and space, a gear must be designed and shown to operate at a profit, markets must be developed, etc. The expense of such an undertaking and the always present finite budget suggest that a very careful allocation of investigatory funds is necessary to optimize the reduction of uncertainty about the economic aspects of harvesting our fishery resources.

A nonoptimal allocation of investigatory funds might be a serious constraint against full resource utilization. We outline here some of the decisional elements that are required in a system for providing information to fishery investors. This system is composed of three segments: policy-formulation, planning, and investigatory.

The policy-formulation segment is based on the axiom that the investigatory entity in itself does not catch, process, or consume fish. The investigatory entity can only sequentially supply information on investment risk and develop methods and strategies by which investment risk can be demonstrably lowered. The investigatory entity clearly produces services rather than goods as its output. The question of to whom these services shall be directed is of primary concern in the policy-formulation segment of the system. The policy-formulation segment, then, identifies the "customers" that will consume the services. The customers include, at least, the fishermen, the processors, and the consumers of fishery products. Policy will specify the degree of interest in each customer group.

Once the customers are identified, their needs must be determined. Perhaps the most objective method of determining the needs of the customers is by "market research." The term in this instance implies that objective techniques will be used to determine the needs of the customers. These needs are, however, almost certain to be dichotomous. The dichotomy is reflected in the difference between the needs of the customers as claimed by the customers and the needs of the customers as viewed by competent industrialists, economists, and biologists. (Excellent examples of this dichotomy in needs may be found in Chapman, 1966.) The actual and overt reconciliation of the needs as seen from the two points of view will do much to reduce many of the institutional barriers discussed by Chapman (1966).

At this point in our system we have established a policy defining certain customer groups and our relative interest in each. In addition we have identified certain rather general needs which both satisfy the customer group and are technically reasonable. A list of informational needs, even for a relatively small region, is likely to be large. Our investigatory entity is faced with a finite budget and cannot possibly cope with or satisfy every need of its customers. A decision must be made with respect to which needs should be satisfied.

A decision with respect to the needs to be initially satisfied can be based on various criteria. One criterion that should be considered is the "return function," which simply relates the output of an endeavor to the cost of achieving the output. Thus the output or return is a function of the input or the expenditure required to achieve the input. The concept of the return function is a much more useful and general concept than the benefit-cost ratio, because the benefit-cost ratio implies that the benefits (the returns) are linearly related to the costs (the inputs) of achieving the benefits—which is not necessarily true. Furthermore, the benefit-cost ratio implies that a zero benefit always has a zero cost—which again is not necessarily true because for some endeavors a threshold cost must be expended before any benefits can accrue. Thus, rather than use the linear benefit-cost function, we use here the more general concept of a return function.

A return function can take almost any reasonable shape. A general shape for a return function is a sigmoid curve: at low levels of input the return is at a low level and nearly constant; once a threshold of input is reached the return increases rapidly and then reaches an asymptote at high levels of input. Conversely, the return is virtually nil from low levels of input, accelerates rapidly at intermediate levels, and diminishes at very high levels. It is within the realm of the policy-formulation segment to make decisions that provide a scale for the return function.

The provision of a scale for the abscissa of the return function is fairly straightforward. It is a scale of dollars and refers to the cost of a single investigational endeavor. Deciding on the scale for the ordinate, however, requires some complex and perhaps difficult decisions. As an example, should return be measured in terms of existing yields or potential yield? The return from a fishery that is already operating at a nearly maximum yield would be negligible compared with that return from fisheries on unexploited or lightly harvested stocks. On the other hand, should return be measured on a scale that reflects a maintenance of yield at some reasonable level? As another example, should returns be measured in terms of development of U.S. fisheries, or, for example, expanding the fisheries of developing nations? In the former instance, the scale might be in pounds of fish; in the latter the scale might be measured in terms of an index of international relations. Many other possible examples involve such questions as the relative importance of food fish versus industrial fish and the related problem of whether return should be measured in tons or dollars.

There are several logical frameworks within which the problem of scale can be resolved. One such framework might involve a consideration of the goods and services produced by the customers. It would be reasonable, in fact, to measure the health of the fishing industry, in the broad sense, by the value of the goods and services that it produces. If we ascribe to the philosophy that the health of the fishing industry can be measured in terms of the goods and services it produces, then some of our decisions with respect to the scale of the argument of the return function become rather clear. Our abscissa would be measured in terms of the cost of an investigatory activity and the ordinate would be measured in terms of the value of the goods and services generated by the information developed by the investigatory activity.

Thus, the formulation of policy is customer oriented. The customers are identified; their needs are researched and reconciled with appropriate technological knowledge, thereby eliminating certain institutional barriers and crystalizing concepts on areas of emphasis; and finally, the scale of return is determined.

The second segment of our system, the planning segment, is resource oriented. Its function is to use the policies formulated in the policy segment to select the resources or activities in our list of needs that enter the investigatory process. The primary element in the planning segment is the resource base, which can be divided into three components: (1) the unidentified or unharvested resources, (2) the lightly fished resources, and (3) the heavily fished resources. From a planning point of view each of these components elicits different questions. For an unidentified or unexploited resource the first question we need to ask is the utility of the resource. There are for example thousands of tons of lanternfish in the oceans. For what can they be used? The concept of utilizing some of the more bizarre marine organisms has its analogy in the terrestrial environment. At present technological and food resource levels, we would simply not think of harvesting components of the terrestrial biomass. Some forest insects, for example, constitute a rather large biomass, are probably quite edible, and could almost certainly be reduced to a nutritious, tasteless protein powder. We can now catch these insects on a small scale, but it should not be difficult to harvest tons of them if we developed appropriate traps, and so on. Just as we might not wish to harvest insects in lieu of some other terrestrial resource, we will not, in planning, wish to consider every organism in the ocean as having immediate utility. Rather, we would probably place first emphasis on harvesting organisms for which a market is known to exist or can easily be developed, and for which a harvesting technology is likely to be available. Another question that concerns an unexploited or unidentified resource is that of its potential value. Naturally emphasis would be placed on resources that have the greatest potential for increasing the goods and services generated in the fishing industry.

The second component of the resource base—the lightly fished resources—elicits questions concerning yield potential and development of more efficient catching mechanisms. The third component—the heavily fished resource—generates questions of maintaining the yield as well as the development of more efficient harvesting techniques.

The planning segment considers as many entities of the resource base as possible and develops return functions for each. The return function is the planner's appraisal of the goods and services that the customer will generate as a result of reduced uncertainty. With the establishment of a set of return functions, it is possible, given a funding level, to choose a subset of the set of resource entities that will maximize the return. It is obvious that the particular members and the number of members in the maximizing subset are a function of the funding level. In actuality, then, the maximizing subset defines those problems, needs, and requirements of the customer to which it is feasible to allocate funds; the feasibility pertains to expected return. If planning has been successful the allocation should result in maximized or near-maximized return.

The actual research on the areas of customer uncertainty is conducted in the investigatory segment of the system. The use of some objective criterion such as the return function ensures that the research has an attainable end product. An example of an end product is the prospectus mentioned earlier. For the development of a fishery the prospectus might include a number of considerations: (1) a description of the operational base. What is the magnitude of the resource? What are the sustainable yields from the resource? Under what weather conditions would the resource need to be harvested? (2) The nature of potential catches. What is the size of the fish? What is the potential catch per set? What is the density of schools or of the fish? What level of catch per fisherman can be expected? (3) The configuration of the fishing platform and the fishing gear. Should the boat operate with one type of gear or several? What is the optimal size of the boat, range, cruising speed, etc.? What is the best size of the net? How should the net be constructed? (4) Maximization of the efficiency of a given boat-gear configuration. What is the relation of the fish to the environment? What are the best search strategies? How can the fishing units cooperate? (5) Industrial logistics. What harbor facilities are necessary? How large should be the processing plant? What is the nature of the labor force? (6) Finally, all of these elements need to be placed together to determine cost structure and feasibility. What can be expected in revenues from catches and what are the operating costs likely to be? Our listing of course is not exhaustive but does include a reasonable sample of the questions that an investor is likely to ask. Provision of this information and the development of new information that reduces operating costs is necessary to the growth of the fishing industry.

The information development system that we have described is not in itself intrinsically important. What is important is that a system be developed. Such a system will eliminate or greatly reduce two constraints on the full utilization of fishery resources: (1) a lack of knowledge concerning the species to be harvested, profitable methods for harvesting the species, etc.—a constraint that discourages investment, and (2) an inefficient attainment of knowledge in which the budgetary allotment of an investigational entity is used inefficiently. An example of an inefficient attainment of knowledge is the conduct of several investigations when the level of funding is sufficient for obtaining a reasonable return from only one or two investigations; it is not difficult to find underfunded investigations. A second example is the question of staff excellence. A staff of excellent researchers will greatly compress the abscissa scale of the return function of an investigation in comparison with the same scale for an investigation conducted by a mediocre staff. The constraint of inefficient acquisition of knowledge reduces the amount of information that can be attained on a fixed budget.

Up to this point we have considered constraints that deal with decision making and information acquisition. Elimination of these constraints will provide substantial increases in catches. Our goal, however, should not be merely to provide substantial increases in catches, but rather to increase the goods and services generated by the fishing industry by some order of magnitude. When we consider this problem our informational constraints are dropped in favor of a much more important constraint: funding. Without really substantial increases in funding it will be impossible to develop a fish harvesting technology that is some order of magnitude more efficient than the nets and hooks now used. The density and mobility of fish populations and labor costs require much more efficient harvesting techniques than those now available. We need a technology that is not dependent on nets and hooks, at least as we traditionally think of them; we need what Alverson and Ego (1966) called "futuristic approaches." We need the sophistication of space in the ocean—and this will be expensive.

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FISHERY RESOURCES OF THE NORTH ATLANTIC AREA

by

ROBERT L. EDWARDS

The North Atlantic area differs from all the others considered here today in that it is already intensively exploited. Nonetheless no one will disagree that it can yield even more, perhaps double the present landings. Further, no one will disagree that to double present landings there must be radical improvements in capture technology, new markets and possibly even a different economic basis for our fisheries. It is our purpose today to delineate the size and nature of the resource as clearly as possible so that others may suggest the appropriate course of action to strengthen the industry.

The American fishery industry never really exploited all the available resources off the Northwest Atlantic coast. That the area could produce very much more was dramatically demonstrated when the USSR began to take an interest in the herring and silver hake stocks in the early 1960's. As a result of Soviet activity alone, the landings from the Gulf of Maine (ICNAF Subarea 5) were more than doubled in a period of five years (Fig. 1). This traditionally American fishing area now plays host to the vessels of many countries and our contribution to the total catch has dropped from 98% or better to barely 32%.

This increased exploitation has had its direct effects. Some of our fisheries are virtually out of business, others are barely maintaining themselves. Some products are now so scarce that the consumer is paying record prices, even luxury prices, for products that once even the humblest could enjoy occasionally. The scientific evidence is clear cut. The overall abundance of those species taken with an otter trawl has dropped 40% in four years. In Table 1 are some comparative catch/tow data obtained during the fall groundfish surveys in the New England area carried out by the Bureau's Laboratory in Woods Hole. Four species are listed separately because they are especially interesting.

Haddock abundance has dropped over 60%. In this case there has been serious overfishing. This species has been regulated (by establishing a minimum mesh size) for maximum yield since 1953. Mesh regulation is premised upon the maintenance of a reasonable stable amount of effort. The fishing fleets of the Soviet Union, and to a lesser degree those of Canada, increased the total fishing mortality on haddock by a factor of about 3 times over a period of two years with the result that almost no one can economically fish for haddock at this time. To add to our grief there have been no substantial year classes recruited to the population since 1963.

Red hake abundance has dropped to about one-fourth its 1964 level. In this case as well the Soviet fishery appears to be the principal cause of the decline. Unlike the haddock however, the red hake does not appear to be seriously overfished. Rather the Soviet fishery is taking all the available surplus before the spring inshore migration and as a result the American industrial fishery based on this species is in dire straits. Silver hake abundance is down moderately. This species normally has wide variations in year class strength and while the data on hand show the effects of fishing, the stocks appear to be in reasonably good shape.

The yellowtail flounder is fished only by Americans at the moment. This species tends to be cyclic in its abundance and there is evidence that colder water temperatures

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THE AUTHOR — *Dr. Edwards is assistant director of the U.S. Bureau of Commercial Fisheries Biographical Laboratory at Woods Hole, Mass.*

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DISTRIBUTION OF THREE SPECIES OF SHRIMP (GENUS *PENAEUS*) IN WATERS CONTIGUOUS TO SOUTHERN FLORIDA[1]

CARL H. SALOMAN
Bureau of Commercial Fisheries Biological Laboratory,
St. Petersburg Beach, Florida 33706

DONALD M. ALLEN AND THOMAS J. COSTELLO
Bureau of Commercial Fisheries Biological Field Station,
Miami, Florida 33149

ABSTRACT

Shrimp of the genus *Penaeus*, collected in the southern Florida—western Bahamas area, were identified to determine species distribution and composition. *Penaeus duorarum* is the dominant species in southern Florida waters and, together with *P. aztecus*, occurs along the lower east and west coasts of the State. *P. brasiliensis* occurs near the Florida Keys and along the east coast of southern Florida, and is apparently the dominant species in the western Bahamas. In Biscayne Bay, Fla., *P. duorarum* was more abundant than *P. brasiliensis* in all catches examined.

INTRODUCTION

The commercial shrimp fishery of southern Florida is based on the pink shrimp, *Penaeus duorarum* Burkenroad. Two closely related species, the Caribbean brown shrimp, *P. brasiliensis* (Latreille), and the brown shrimp, *P. aztecus* (Ives), also occur in this region but are of minor importance. The three are difficult to distinguish and were considered a single species (*P. brasiliensis*) prior to taxonomic revision by Burkenroad (1939).

The purpose of this report is to summarize available information on the geographic distribution of *P. duorarum, P. brasiliensis,* and *P. aztecus* in the waters of southern Florida and the western Bahamas (24°–27°00′N and 77°30′–83°00′W), with particular emphasis on their occurrence in Biscayne Bay, Fla. (Fig. 1).

PROCEDURE

Shrimp examined from the survey area were collected from shrimp fishermen, from mark-recovery experiments conducted by the Bureau of Commercial Fisheries, and from exploratory fishing operations of the M/V SILVER BAY (Fig. 1). Most shrimp from shallow water were taken

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[1] Contribution No. 36 from the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.

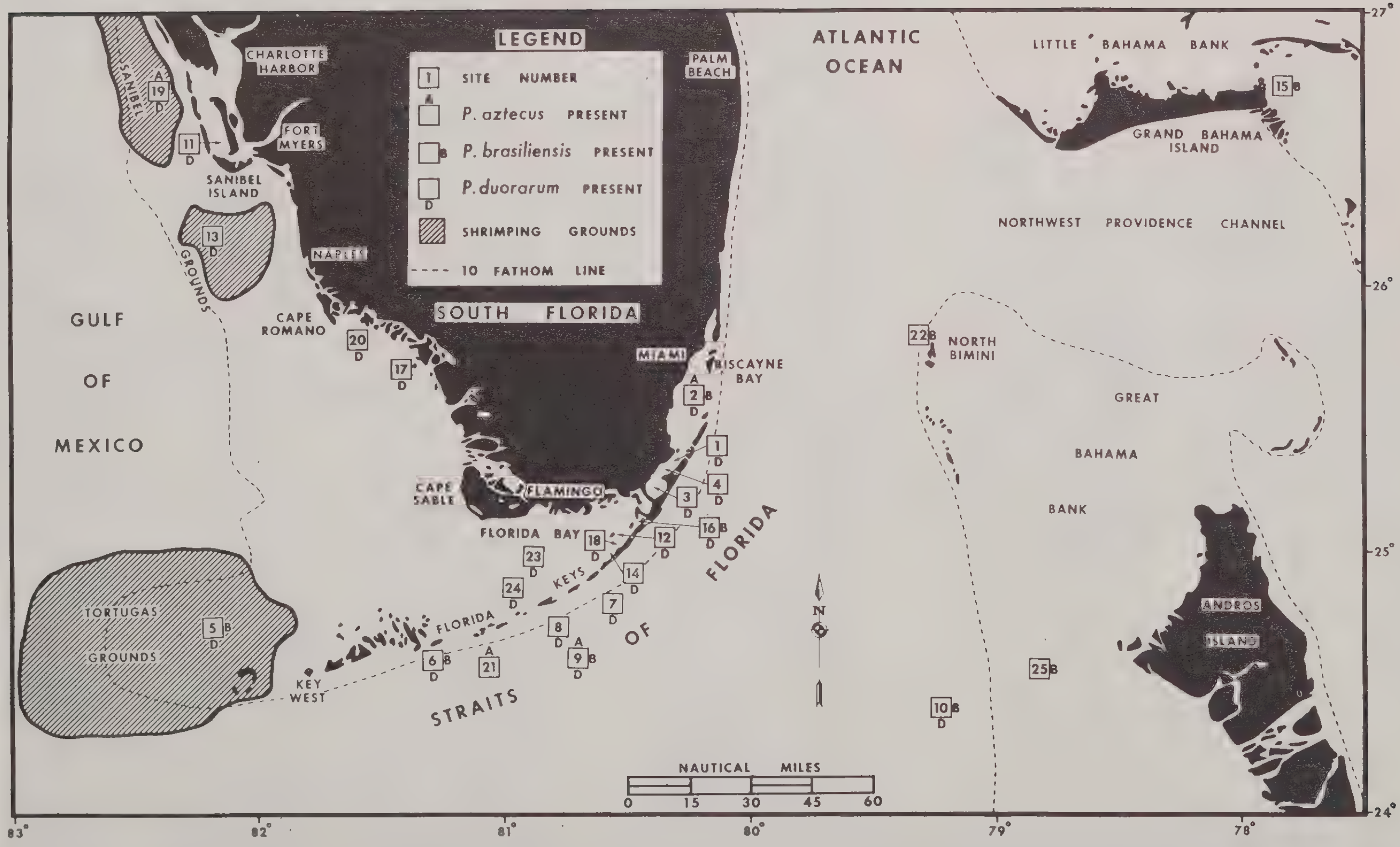
LEGEND
1 SITE NUMBER
A P. aztecus PRESENT
B P. brasiliensis PRESENT
D P. duorarum PRESENT
SHRIMPING GROUNDS
10 FATHOM LINE
ATLANTIC OCEAN
LITTLE BAHAMA BANK
GRAND BAHAMA ISLAND
NORTHWEST PROVIDENCE CHANNEL
NORTH BIMINI
GREAT BAHAMA BANK
ANDROS ISLAND
GULF OF MEXICO
CHARLOTTE HARBOR
FORT MYERS
SANIBEL ISLAND
SANIBEL
GROUNDS
NAPLES
CAPE ROMANO
SOUTH FLORIDA
PALM BEACH
MIAMI
BISCAYNE BAY
CAPE SABLE
FLAMINGO
FLORIDA BAY
FLORIDA KEYS
KEY WEST
TORTUGAS GROUNDS
STRAITS OF FLORIDA
N
NAUTICAL MILES
0 15 30 45 60
27°
26°
25°
24°
83°
82°
81°
80°
79°
78°
1 D
2 A B D
3 D
4 D
5 B D
6 B D
7 D
8 D
9 A B D
10 B D
11 D
12 D
13 D
14 D
15 B
16 B D
17 D
18 D
19 A D
20 D
21 A
22 B
23 D
24 D
25 B

FIGURE 1. Occurrence of *P. duorarum*, *P. brasiliensis*, and *P. aztecus* in southern Florida and the western Bahamas.

in frame trawls, and those from deeper water in otter trawls. Large numbers were collected from the Tortugas grounds over a period of several years; most, however, were from depths less than 20 fms (36.6 m). Consequently, the absence of a species from the Tortugas collections does not necessarily imply its absence from deeper waters of the Tortugas grounds.

Samples of *Penaeus*, examined to determine species composition of shrimp populations in Biscayne Bay, were obtained from a commercial bait shrimper. The shrimp were caught by three to four boats which fished portions of 30 square miles in south Biscayne Bay. The shrimp were sampled with a fine-meshed dip net from a holding tank soon after capture. There was no consistent seasonal difference in fishing areas, and no observed differential mortality between *Penaeus* species during the period after capture and before sampling. They were collected monthly from October, 1960, through September, 1961, and in June and October, 1963.

Specimens were identified to species under a dissecting stereomicroscope by the criteria of Burkenroad (1939). No attempt was made to distinguish subspecies.

AREAL DISTRIBUTION BY SPECIES

Penaeus duorarum.—This species is common in the estuaries and shallow marine waters surrounding southern Florida. *P. duorarum* has also been reported from depths to 60 fms (109.7 m) southeast of the Florida Keys, and to 200 fms (365.8 m) off the western edge of the Great Bahama Bank (Bureau of Commercial Fisheries, 1961). Burkenroad (1939) reported on the distribution of *P. duorarum*, and later Costello & Allen (1966) summarized other reports on distribution in southern Florida.

In our survey, *P. duorarum* was the only member of the genus in samples from the south Sanibel grounds (site 13)[2], coastal Florida from Pine Island Sound southward (sites 11, 20, and 17), and western Florida Bay (sites 23 and 24). It was the dominant species from the Tortugas grounds (site 5), eastern Florida Bay (sites 14, 18, 12, and 16), and the coastal waters of southeastern Florida (sites 6, 8, 9, 7, 3, 4, 1, and 2). This species occurred in deep water off the western edge of the Great Bahama Bank (site 10), but was not found in samples from shallower water on the western Bahama Banks (sites 15, 22, and 25).

Penaeus brasiliensis.—This species was first reported in waters of southern Florida (Biscayne Bay) by Eldred (1960), and later in the same area by Iversen & Van Meter (1964). It has been collected in deeper water off the western edge of the Great Bahama Bank in 200 fms (365.8 m) (Bureau of Commercial Fisheries, 1961).

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[2] All references to sites apply to Figure 1 and Table 1.

TABLE 1

Species Composition of *Penaeus* Samples from Southern Florida and the Western Bahamas, 1959–66

				Numbers		
Collection site	Site number[1]	Date	Depth (meters)	*Penaeus duorarum*	*Penaeus brasiliensis*	*Penaeus aztecus*
Card Sound	1	1959	1.8–3.7	10	0	0
Biscayne Bay	2	Feb., 1959, to Oct., 1963	1.8–3.7	2140	314	1
Barnes Sound	3	July, 1959	1.8–3.7	66	0	0
		May, 1961	1.8–3.7	56	0	0
Little Card Sound	4	Aug., 1959	1.8–3.7	34	0	0
Tortugas Grounds	5	Dec., 1959, to March, 1966	14.6–49.4	2872	1[2]	0
Hawk Channel	6	Feb., 1960	12.8	98	4	0
East of Lower Matecumbe Key (M/V Silver Bay Station 2373)	7	Oct., 1960	36.6	13	0	0
South of Lower Matecumbe Key (M/V Silver Bay Station 2388)	8	Oct.,1960	73.2	94	0	0
South of Lower Matecumbe Key (M/V Silver Bay Station 2390)	9	Oct., 1960	91.5	13	4	11
Off western edge of Great Bahama Bank (M/V Silver Bay Station 2470)	10	Nov., 1960	228.6	60	76	0
Pine Island Sound	11	Nov. to Dec., 1960	1.8–3.7	711	0	0
Bottle Key (eastern Florida Bay)	12	Nov., 1960, to Jan., 1961	1.8	234	0	0
South Sanibel Grounds	13	Jan., 1961, to April, 1963	9.1–18.3	1040	0	0
Snake Creek (eastern Florida Bay)	14	Feb., 1961	1.8	81	0	0
Grand Bahama Island	15	Sept., 1961	1.8	0	6	0
Buttonwood Sound (eastern Florida Bay)	16	Oct., 1961	1.8–3.7	27	0	0
		Jan., 1962	1.8–3.7	21	1	0
Pavilion Key	17	Nov., 1961	1.8–3.7	29	0	0
Cowpens Cut (eastern Florida Bay)	18	Jan., 1962	1.8	32	0	0
Northwest Sanibel Grounds	19	June, 1962	11.0	–	–	2[2]
		Nov., 1962	11.0	1[2]	–	–
Indian Key	20	Aug. to Sept., 1962	1.8–3.7	231	0	0
South of Vaca Key	21	Jan., 1963	60.4	–	–	3[2]
North Bimini	22	May, 1963	20.1	0	1	0
Schooner Bank (western Florida Bay)	23	July, 1963	1.8	76	0	0
Tripod Bank (western Florida Bay)	24	Aug., 1963	1.8	94	0	0
Andros Island	25	Mar., 1964	5.5–7.3	0	6	0

[1] Site numbers refer to Figure 1.

[2] Selected from shrimp catch of fishermen. Catch not examined for other species.

Results of our survey indicate that *P. brasiliensis* is restricted primarily to the southern and eastern sectors of the survey area. Only one specimen was found among the many Tortugas shrimp examined (site 5) and only one specimen occurred in samples from Florida Bay (site 16). Samples from Biscayne Bay (site 2) in summer and early fall contained relatively high percentages of *P. brasiliensis*. Additional specimens were obtained southeast of the Florida Keys (sites 6 and 9). The species was in even deeper water off the western edge of the Great Bahama Bank (site 10), and was the only species in three small samples from the shallower water of the western Bahama Banks (sites 15, 22, and 25).

Penaeus aztecus.—This species was first recorded in southern Florida waters (Key Largo) by Burkenroad (1939)[3]. Tabb & Manning (1961) found small numbers of juveniles in Buttonwood Canal near Flamingo in northern Florida Bay. Adult specimens were reported in 50 to 60 fms (91.4 to 109.7 m) southeast of the Florida Keys (Bureau of Commercial Fisheries, 1961), and Eldred, Williams, Martin, & Joyce (1965) reported one postlarva from the Gulf of Mexico, 60 miles (96.6 km) west of Fort Myers.

Within the survey area, *P. aztecus* was collected from the northwest Sanibel grounds (site 19) and from relatively deep water southeast of the Florida Keys (sites 9 and 21). A single specimen was collected in Biscayne Bay (site 2). None was recorded from the south Sanibel or Tortugas grounds or from the western Bahamas. Although Tabb & Manning (1961) reported *P. aztecus* from northern Florida Bay, none was obtained in our survey from Pine Island Sound southward along the Florida west coast or in Florida Bay.

SEASONAL SPECIES COMPOSITION IN BISCAYNE BAY

Of 2,020 shrimp from Biscayne Bay that were examined and identified at monthly intervals, October, 1960–September, 1961, 86.4 per cent were *Penaeus duorarum*, and 13.6 per cent *P. brasiliensis*. *P. aztecus* was represented by a single specimen taken in October, 1960 (Table 2).

P. duorarum was more abundant than *P. brasiliensis* every month and constituted over 98 per cent of the catch from November-May. *P. brasiliensis* was taken in all months except December, April, and May, but in greatest numbers in June-October; in July, it accounted for 41 per cent of the sample. Other collections by the authors and previous studies by Eldred (1960) and Iversen & Van Meter (1964) showed that at least a few *P. brasiliensis* occur in Biscayne Bay in December, April, and May. The seasonal ratio that we found between *P. duorarum* and *P. brasiliensis* in Biscayne Bay is further corroborated by Eldred (personal communica-

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[3] Pérez Farfante (1967) questions the validity of this observation.

TABLE 2

Species Composition of Bait Shrimp Catches in Biscayne Bay, Florida—1960, 1961, and 1963[1]

Month	Number in samples			Percentage by species	
	Penaeus duorarum	*Penaeus brasiliensis*	Total	*Penaeus duorarum*	*Penaeus brasiliensis*
1960					
October	75	19	94	79.8	20.2
November	123	1	124	99.2	0.8
December	101	0	101	100.0	0
1961					
January	102	2	104	98.1	1.9
February	110	2	112	98.2	1.8
March	92	1	93	98.9	1.1
April	120	0	120	100.0	0
May	163	0	163	100.0	0
June	84	20	104	80.8	19.2
July	216	148	364	59.3	40.7
August	276	34	310	89.0	11.0
September	282	48	330	85.5	14.5
Subtotal for 12 consecutive months	1744	275	2019	86.4	13.6
1961					
October	238	11	249	95.6	4.4
1963					
June	93	11	104	89.4	10.6
October	65	17	82	79.3	20.7
Total	2140	314	2454	87.2	12.8

[1] Does not include a single specimen of *P. aztecus* taken October, 1960.

tion). Her samples of December, 1959, contained 97 per cent *P. duorarum* and 3 per cent *P. brasiliensis*; in contrast, a July, 1960, sample had 67 per cent *P. duorarum* and 33 per cent *P. brasiliensis*. Our additional bay samples in October, 1961, and June and October, 1963, indicate little change in species composition from year to year (Table 2).

Acknowledgments

We are indebted to Messrs. Robert Still and A. J. Mills, bait shrimpers, and Harvey R. Bullis, Jr., Bureau of Commercial Fisheries, for furnishing samples of shrimp. We also thank Dr. Enrique E. Boschi, Buenos Aires, Argentina, for verifying our identification of specimens and Mrs. Bonnie Eldred, Florida Board of Conservation, for information concerning *Penaeus brasiliensis* in Biscayne Bay, Fla.

SUMARIO

DISTRIBUCION DE TRES ESPECIES DE CAMARONES (GENERO *Penaeus*) EN AGUAS CONTIGUAS A LA PARTE SUR DE LA FLORIDA

Se resume la distribución conocida de *Penaeus duorarum, P. brasiliensis* y *P. aztecus* para el área sur de la Florida y oeste de las Bahamas (24°00′–27°00′N y 77°30′–83°00′0). *P. duorarum* se presenta en todas las aguas que bordean el sur de la Florida. Es el principal miembro del género en el área de Sanibel y las Tortugas, en las aguas costeras del sudoeste de la Florida y en la Bahía de Florida. *P. duorarum* se mantiene dominante a lo largo de la costa sudeste de la Florida, en la Bahía de Biscayne y en aguas más profundas al sudeste de los Cayos de la Florida, pero la incidencia de *P. brasiliensis* aumenta. Al este, en las Bahamas occidentales, un muestreo preliminar indica que *P. brasiliensis* es dominante. Han aparecido con poca frecuencia ejemplares de *P. aztecus* en el área noroeste de Sanibel, en la parte norte de la Bahía de Florida, cerca de Cayo Largo y en la Bahía de Biscayne. Esta especie es aparentemente más común en las aguas más profundas al sudeste de los Cayos de la Florida, donde está asociada con *P. duorarum* y *P. brasiliensis*.

En la Bahía de Biscayne, ambas especies *P. duorarum* y *P. brasiliensis* se presentan durante todo el año y *P. aztecus* es raro. Basándonos en nuestras observaciones, *P. duorarum* es la especie más abundante todos los meses y constituye más del 98 por ciento de la pesca de noviembre a mayo. Los mayores por cientos de *P. brasiliensis* en pescas realizadas durante nuestro estudio fueron de junio a octubre; el máximo fue 41 por ciento en julio.

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Photomicrographic studies on amoeboid protozoa from the American and Pacific oyster. **Thomas K. Sawyer,** U. S. Bureau of Commercial Fisheries, Biological Laboratory, Oxford, Maryland.

Two species of protozoa with morphologic characters similar to amoebae, proteomyxans, and slime molds have been isolated from tissues and mantle fluids of oysters from Maryland (*Crassostrea virginica*) and British Columbia (*Crassostrea gigas*). These organisms have been studied with phase contrast photomicrography and with histologic stains to record the variable nature of nuclei and trophic stages.

The Canadian organism is very transparent and is easily overlooked in liquid media. Fusion occurs on agar media, and protoplasmic masses of variable size are abundant in culture. Trophozoites and plasmodia have delicate filose pseudopodial projections, and contain one to 30 nuclei. This organism shows affinities to the genus *Flabellula* (amoeba), *Biomyxa* (proteomyxan), and *Arachnula* (proteomyxan). The Maryland organism resembles *Vahlkampfia calkensi* Hogue and *V. patuxent* Hogue and has shown nucleolar fragmentation similar to that seen in the slime molds *Echinosteliopsis oligospora* and *Acrasis rosea.*

Both organisms grow at 5 C, feed on a variety of bacteria and yeasts, fail to grow in distilled water, and rarely form cysts. Promitosis, metamitosis, amitosis, and other observations on such nuclear activity in these organisms have been studied.

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Cladocera and Copepoda in McNary Reservoir, 1965-66

John F. Scarola

John F. Scarola

Bureau of Commercial Fisheries
Biological Laboratory
2725 Montlake Boulevard East
Seattle, Washington

Cladocera and Copepoda in McNary Reservoir, 1965-66

A limnological study of McNary Reservoir was undertaken by the Bureau of Commercial Fisheries in 1965-66, but a comprehensive report at this time would be premature. This paper summarizes briefly the methods and findings of the work in relation to the Cladocera and Copepoda.

Study Area and Methods

McNary Reservoir is in Oregon and Washington on the main stem of the Columbia River, 292 miles above the river mouth (U.S. Army Corps of Engineers, 1946, 1952). It was formed in 1957 at the completion of McNary Dam, which is operated by the U.S. Army Corps of Engineers. The reservoir lies in a semi-arid region used primarily for grazing and cultivation; flowing through the area are three major tributaries, the Walla Walla, Snake, and Yakima rivers.

The basic physical features of McNary Reservoir are:

Normal pool elevation (m.s.l.)	340 feet
Normal pool length	59 miles
Normal pool area	37,900 acres
Shoreline	242 miles
Maximum width	9500 feet
Maximum depth	120 feet
Average depth	65 feet
Volume	1,345,000 acre feet

Sampling, conducted from August 1965 through September 1966, was at one- or two-week intervals during the summer but was irregular during the other seasons. Plankton collections were made at 24 sampling stations, at which water depth ranged from about 20 to 85 feet. The entire water column was sampled by a vertical haul at each station.

A half-meter Nansen-type net, constructed of No. 10 monofilament nylon bolting cloth, was used; the samples were preserved in 5 per cent formalin, identified, and enumerated in terms of organisms per cubic meter.

Species and Relative Abundance

Twenty-four species of Cladocera and Copepoda were collected, which represented 13 and 6 genera, respectively (Ward and Whipple, 1963). More species of Cladocera (17) than Copepoda (7) were found, but as a group the cladocerans were usually outnumbered by the copepods. The species taken in McNary Reservoir were:

- I. Order Cladocera
  - 1. Family Leptodoridae
    - *Leptodora kindtii* (Focke) 1844
  - 2. Family Sididae
    - *Sida crystallina* (O. F. Müller) 1875
    - *Diaphanosoma brachyurum* (Liéven) 1848
  - 3. Family Daphnidae
    - *Daphnia galeata* Sars 1864 *mendotae* Birge 1918
    - *Scapholeberis kingi* Sars 1903
    - *Ceriodaphnia pulchella* Sars 1862
  - 4. Family Bosminidae
    - *Bosmina longirostris* (O. F. Müller) 1785
  - 5. Family Macrothricidae
    - *Ilyocryptus sordidus* (Liéven) 1848
    - *Macrothrix laticornis* (Jurine) 1820
  - 6. Family Chydoridae
    - *Monospilus dispar* Sars 1861
    - *Leydigia quadrangularis* (Leydig) 1860
    - *Alona quadrangularis* (O. F. Müller) 1785
    - *Alona costata* Sars 1862
    - *Pleuroxus denticulatus* Birge 1878
    - *Pleuroxus trigonellus* (O. F. Müller) 1785
    - *Pleuroxus aduncus* (Jurine) 1820
    - *Chydorus sphaericus* (O. F. Müller) 1785
- II. Order Copepoda
  - A. Suborder Calanoida
    - 1. Family Temoridae
      - *Epischura nevadensis* Lilljeborg 1889
    - 2. Family Diaptomidae
      - *Diaptomus ashlandi* Marsh 1893
  - B. Suborder Cyclopoida
    - 1. Family Cyclopoidae
      - *Cyclops vernalis* Fishcher 1853
      - *Cyclops bicuspidatus* Claus 1857 var. *thomasi*
  - C. Suborder Harpacticoida
    - 1. Family Canthocamptidae
      - *Mesochra alaskana* M. S. Wilson 1958
      - *Canthocamptus staphylinoides* Pearse 1905
      - *Bryocamptus zschokkei* (Schmeil) 1893

Cyclopoids[1] ranked first in abundance. Numbers increased gradually in the spring, peaked in late August and early September, declined slightly later in September, and then increased to a less pronounced peak in October. The population dropped off rapidly in late fall and remained relatively low throughout the winter and early spring.

Seasonal variation of *Bosmina,* second in abundance, was almost identical to that of the cyclopoids, except that the spring increase occurred more rapidly and the population peak was reached slightly earlier—in July and early August. The seasonal variation of *Daphnia,* third in abundance, was not significantly different from the cyclopoids or *Bosmina.* The calanoids ranked fourth; numbers remained consistently high throughout the spring and summer and then decreased markedly in the fall. Although sampling data were limited in the winter, population levels appeared to be similar to those in the spring and summer.

Alona, Sida, Ceriodaphnia, and *Pleuroxus* followed typical patterns of seasonal change, generally building up in the spring, peaking in the summer, and decreasing in the fall.

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[1] In enumeration, the Copepoda were identified to suborder and the Cladocera to genera.

A notable exception was *Illyocryptus*; its population was low in the winter and summer and high in the spring and fall. *Chydorus* remained stable throughout the year. *Leptodora*, the largest of the cladocerans, appeared sporadically in the summer and fall.

The relative abundance of organisms by percentage showed that in the spring, summer, and fall, cyclopoids and *Bosmina* constituted the major portion of the population. Calanoids constituted the largest segment of the population in the winter.

The numbers of the remaining Cladocera and Copepoda collected were small and constituted only a minor portion of the total population. All Cladocera with the exception of *Monospilus dispar* have been reported in the state of Washington.[2]

Acknowledgments

I thank Rufus W. Kiser, Centralia Junior College, Centralia, Washington, and Harry C. Yeatman, University of the South, Sewanee, Tennessee, for identification of the Cladocera and Copepoda.

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[2] "Cladocera of Washington," presented by Rufus W. Kiser at the 31st Annual Meeting of the Northwest Scientific Association, Spokane, Washington, December 27, 1957.

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Folsom Plankton Splitter Modified for Enumeration of Entomostraca

The Folsom plankton splitter described by McEwen, Johnson, and Folsom (1954) was originally used for the subsampling of marine zooplankton. The splitter is a rotating cylindrical drum with a vertical, semicircular partition mounted in the center. The drum is supported by two legs fastened to a base plate, fitted with leveling screws and a spirit level. A plankton sample is poured into the drum. When the drum is rotated, the partition splits the sample.

When this splitter was used to enumerate freshwater zooplankton, namely entomostracans, organisms were frequently lost in manipulation and removal of the subsam-

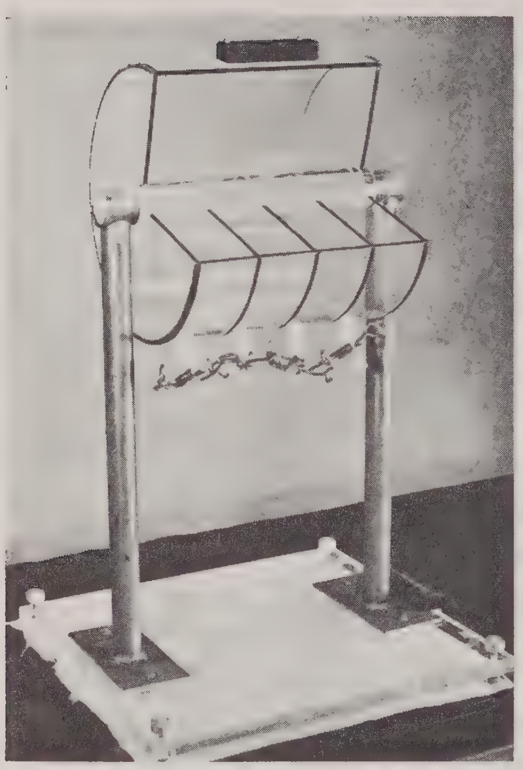

FIG. 1. Modified Folsom splitter showing drain tubes and clamps.

ple. To reduce these losses we modified the splitter by providing four splitting chambers instead of the original two and by replacing the pouring spouts with individual chamber drains fitted with pieces of rubber tubing and pinch clamps (Fig. 1).

To determine that the instrument was accurately constructed, 250 ml of water (a good working volume) was split on five trials. Chamber volumes did not deviate more than 1.2% from the expected volume despite loss of water in draining and measurements; a ratio of mean squares, calculated by analysis of variance, showed no significant differences among the chambers at the 0.05 level.

Chi-square values for tests with plankton samples (containing approximately 350 organisms) showed that the differences in distribution among the four chambers in a single splitting operation were not significant in 9 of 10 trials (0.05 level). The pooling of chi-square values in 10 tests indicated no significant difference among mean values of counted organisms in the four chambers.

This modification has proved satisfactory. Eliminating unnecessary and cumbersome operations has greatly reduced sample loss. Construction details are available from the authors.

JOHN F. SCAROLA
ANTHONY J. NOVOTNY

*U.S. Bureau of Commercial Fisheries,
Fish-Passage Research Program,
2725 Montlake Boulevard East,
Seattle, Washington 98102.*

REFERENCE

MCEWEN, G. F., M. W. JOHNSON, AND T. R. FOLSOM. 1954. A statistical analysis of the performance of the Folsom plankton splitter based on test observations. Arch. Meteorol. Geophys. Bioklimatol., Ser. A, **7**: 502–527.

THE MARINE MAMMALS

of the North-western Coast of North America

Described and illustrated

Together with an account of

THE AMERICAN WHALE-FISHERY

by Charles M. Scammon

with a new Introduction by
VICTOR B. SCHEFFER
Bureau of Commercial Fisheries
U. S. Fish and Wildlife Service
Seattle, Washington

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INTRODUCTION

TO THE DOVER EDITION

CHARLES MELVILLE SCAMMON (1825–1911) wrote one book, and it has fascinated seafaring men, historians, and naturalists for 94 years. I am told by Joel W. Hedgpeth[1] that the book was a financial failure, and that Scammon used to buy copies from the San Francisco printer at cost of the paper to give to his friends. The unsold copies were lost in the earthquake and fire of 1906. Today the book is very rare; it seldom appears on the book market, where it commands a price of $100 or more.

Who was this man, Scammon? Very little biographical information is available.[2,3] Born in Pittston, Maine, on 28 May 1825, he was younger brother of Jonathan Young Scammon, lawyer, legislator, financier, and civic leader in Chicago. He sailed for California in 1850. In his book we first see him at age twenty-seven, watching the "banded seals" on the California coast at Point Reyes. In another essay[4] he may hint at an earlier life as a disenchanted gold-digger in the following words:

> Among the multitude of adventurers who came hither were a class of industrious, energetic, and hardy men, who, from childhood, had passed their time on board the pigmy fishing-vessels, amid the gales, fogs, and rough seas of the Atlantic, varied only by brief respites at home among friends and companions, who shared their precarious earnings. The change from the life of a mariner to that of a miner was not always congenial to these men, whose hereditary avocations were of the sea. Some restless spirits, unsuccessful in gold-hunting, longed to be again afloat. For this reason, there was no lack of experienced hands ready to embark in any marine venture, even in those gold-digging days.

In 1852 Scammon took "command of a brig, bound on a sealing, sea-elephant, and whaling voyage" (this book, p. 11). Starbuck's history[5] shows that the brig *Mary Helen*, 160 tons, left San Francisco on 1 April 1852 under Captain Scammon, bound for "elephanting." She returned on 26 August with 350 barrels of "elephant," which would have been oil rendered from the elephant seals of southern California and northern Mexico. Scammon's travels during the next two decades, capped by the writing of his book, are imperfectly known. I have pieced together a rough account, largely from remarks in *Marine Mammals*, and in his articles in the *Overland Monthly* from 1869 to 1872.

He may have gone on to the Galapagos Islands and Peru in 1853; certainly he was whaling off Panama in March of that year. He whaled in or near the lagoons on the west side of Baja California, where the gray whales still breed, from 1853 to 1860. In 1855 he discovered the shallow, hidden Laguna Ojo de Liebre which is shown today on most English-language maps as Scammon's Lagoon.[6] His ship at the time of the famous discovery was evidently the *Leonore*, 370 tons, which sailed from San Francisco on 3 December 1855 and returned on 25 July 1856 with 60 barrels of "sperm-oil" and 500 barrels of "whale-oil."[5]

Shortly after the outbreak of the Civil War in 1861 Scammon took command, on the first of May, of a revenue cutter in San Francisco. He attained the rank of captain on 11 July 1864, "when the U.S. Coast Guard was known as the Revenue Service, but before he retired [from disability] in 1895 it was known as the U.S. Revenue Cutter Service and retained that identity until 1915 when it received its present name."[7] As "Captain, U.S.R.M., Chief of Marine Western Union Telegraph Expedition, 1865 and 1866," he traveled to Plover Bay (Siberia), to Norton Sound (Alaska), and to other points in the Bering Sea. Shortly thereafter he published "Notes on the Russian American Company's Trading Posts, etc."[8] William Healey Dall (1845–1927) of the Smithsonian Institution was on this expedition, and in 1870 he named Scammon Bay, Alaska, in honor of his captain.

At times from 1868 to 1870 Scammon visited the Strait of Juan de Fuca, between Washington and Vancouver Island. Here in October 1870 he collected the type specimen of the Davidson piked whale, *Balaenoptera davidsoni* Scammon, 1872.[10] He did not try his hand again at systematic zoology.

Later he must have returned to California, for his entries from 1871 to 1873 refer to ports between Santa Barbara and San Francisco. Louis Agassiz (1807–1873) spent some weeks in San Francisco in 1872;[1] since *Marine Mammals* was subsequently dedicated to his memory, Scammon probably met the famous zoologist in that year. He dated the preface of the book May 1874.

I will not follow his career beyond this point, except to point out that he was stationed in Florida in 1880 in command of the *John A. Dix*, a side-wheel steamer. He wrote about the manatee there, though his notes were not published until 1954.[11]

Charles M. Scammon 1825–1911
Official U. S. Coast Guard Photograph

To a historian I leave the task of writing a full biography of Scammon, and I turn now to his book. "The chief object in this work," he wrote, "is to give as correct figures of the different species of marine mammals . . . as could be obtained from a careful study of them from life, and numerous measurements after death . . ." (this book, p. 11). He lived in an era of *descriptive* zoology.

The concept of a book on seals, sea otters and whales was slowly taking shape in his active mind during his first decade on the west coast. Not until 1862, I think, did he start to measure and to sketch the objects of his interest. Off Baja California that year his men captured three blackfish, and Scammon described the largest one (this book, p. 86). He obtained some measurements of marine mammals (e.g., those of a bowhead and a humpback) from friendly sea captains. I suppose he alerted his cronies to the need for scientific information on the animals they were clubbing, shooting, and harpooning.

In writing his first scientific article he called upon Edward Drinker Cope (1840–1897), who had been named a curator of the Philadelphia Academy of Natural Sciences in 1865. Cope not only edited but also contributed substantially to the report on the cetaceans of the western coast of North America.[12] It is a curious report by modern zoological standards, though typical of its day. Cope, the museum man, was concerned with dry bones and teeth; Scammon the field man, with behavior of the animals, ways of hunting them, and the glamor surrounding the hunt. In this report we see the essential framework of the whale chapters of *Marine Mammals*. When, later, the book itself was being composed, Scammon turned to another expert for help on the systematics of marine mammals, Dall of the Smithsonian.

Also, Scammon began in 1869 to publish a series of short articles in the *Overland Monthly* in the distinguished company of Mark Twain and Bret Harte. His first contribution contained information on the Pribilof Islands of Alaska, which Scammon may have visited in 1868.[13] It was followed by seventeen articles in this journal through July of 1872, at which time he turned his full attention to this book. Eight of the articles dealt with marine mammals—the others with travel scenes, descriptions of lumbering and cod-fishing, the story of Chief Seattle, and so on. The *Overland Monthly* was a magazine of considerable artistic merit. It was published from 1870 to 1875 by John H. Carmany, of San Francisco, who also published Scammon's book.

The main value of *Marine Mammals* lies in its historical, rather than zoological, content. It is a unique segment of Americana. It was published in the year when we Americans tried to save the wild bison. (A bill to "impose a penalty on every man, red, white or black, who might wantonly kill buffaloes" was passed by both houses of Congress but was pocket-vetoed by President Grant.)[14]

Where else can one find a picture like the frontispiece "Whaling Scene in the California Lagoons" or (Plate V) "California Grays among the Ice"?[15] Where else can one find such wealth of detail on methods of the whale fishery from open boats in the North Pacific? I suggest that you read, for example, the dramatic story of Scammon's first attempt to capture gray whales (this book, p. 263). When the first boat returned to the ship "with her freight of crippled passengers, it could only be compared to a floating ambulance crowded with men—the uninjured supporting the helpless." Scammon had been whaling for sixteen years when Svend Foyn, in the North Atlantic, perfected the big harpoon with an explosive head which was to revolutionize whale fishery and finally, in our time, to bring commercial extinction to the blue whale, the greatest animal that has ever lived.

With respect to the zoological content of the book, information far more accurate and more comprehensive has been obtained since 1874. Nonetheless, Scammon wrote of populations, like the sea otters of Washington and Oregon, which were later exterminated. We can see them now through his eyes. When he hunted the gray whales in their breeding waters, they numbered perhaps 25,000; a century later they were nearly gone. Though they are now recovering under strict protection, the shores of Scammon's Lagoon will never again resound to the cries of the whalemen as he heard them in the 1850's.

VICTOR B. SCHEFFER
Bureau of Commercial Fisheries
U.S. Fish and Wildlife Service
Seattle, Washington

NOTES

1. Resident Director, Marine Science Laboratory, Oregon State University, and a keen student of the history of science. Some years ago he interviewed the late L. N. Scammon, son of Charles Melville Scammon. I thank Dr. Hedgpeth for help with this introduction.
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8. U.S. Congress, House. 1868. St. Paul's Island, Alaska . . . 40th Congr., 2d Sess., House Misc. Doc. 131, p. 12.
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13. Scammon, Charles M. 1869. "Fur seals." *Overland Monthly*, 3(5), pp. 393–399.
14. Hornaday, William T. 1931. *Thirty Years War for Wild Life*. Chas. Scribner's Sons, New York, p. 247.
15. Despite the signature "C. M. Scammon, del.," I suspect that he had but a minor part in preparing the figures, for his earlier sketches are crude by comparison. He admits as much (this book, p. 12) by crediting Mr. Steinegger for the "excellent sea and landscape backgrounds."

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A Time-Sequence Oceanographic Investigation in the North Pacific Trade-Wind Zone

GUNTER R. SECKEL

Bureau of Commercial Fisheries Biological Laboratory
Honolulu, Hawaii

INTRODUCTION

The Bureau of Commerical Fisheries Biological Laboratory in Honolulu initiated an oceanographic investigation to gain an understanding of the mechanisms producing changes in the properties and water masses of the trade-wind zone of the North Pacific Ocean. The Bureau undertook this study because changes in the distribution of water masses near Hawaii directly affect the availability of skipjack tuna (*Katsuwonus pelamis*) in a predictable manner [*Seckel*, 1963]. Therefore, both for ecological studies and for predicting favorable environmental conditions, it is important to understand first the basic structure and mechanism of change in the ocean.

A study dealing with changes in the distribution of properties and water masses in the sea requires consideration of the theory of the distribution of variables for heat, salt, and momentum budgets [*Sverdrup et al.*, 1942]. Involved are heat and water exchange at the sea surface, the wind stress, and the effects of water motion in advection and mixing; also essential is a knowledge of the local time change of properties.

A program providing data from which elements of the various budgets can be derived has been designed, and a pilot study to test sampling and processing techniques and to develop methods of analysis is in progress. The initial field phase of the pilot study lasted from February 1964 to July 1965. During this period a grid of hydrographic stations was occupied monthly in the trade-wind zone of the North Pacific near Hawaii.

This study, 'Trade-Wind Zone Oceanography Pilot Study,' is described below. The descriptive phase of analysis of data obtained during these cruises is now under way. The principal descriptive features found thus far are presented here for the vertical structure and the distribution of properties and water masses, in time and space, of the North Pacific trade-wind zone study area. Detailed analyses of this material are to be published separately.

THE FIELD PROGRAM

The pilot study area is bounded by 10° and 26.5°N latitude and by 148° and 157°W longitude. It was chosen for its proximity to the Hawaiian Islands and because it brackets the principal water types and currents of the North Pacific trade-wind zone (Figure 1).

Timing and spacing of samples used in the 'budget' calculations depend upon the period of interest and the nature of the distribution in question. Interest in the trade-wind zone oceanography investigation lies primarily in determining the annual cycle and the annually repeating processes. Heat budget calculations in the pilot study area have shown that seasonal changes in surface temperature occur as a result of well-defined, annually repeating processes [*Seckel*, 1962]. Among these processes the net heat exhange across the sea surface is dominant, but advection also plays an important role. There are four principal advection periods: one during March and April brings warmer water into the island area, and three periods during June and July, October and November, and January and February introduce colder water. The seasonal processes and the periodic influxes of water specify the time interval between samples. If the heat budget were concerned only with the process of net heat exchange across the sea surface, a 2-month interval between samples would probably be adequate. To define the annually repeating advection processes, however, a monthly interval or less is necessary.

For this investigation, the spacing between stations and the vertical spacing of samples at

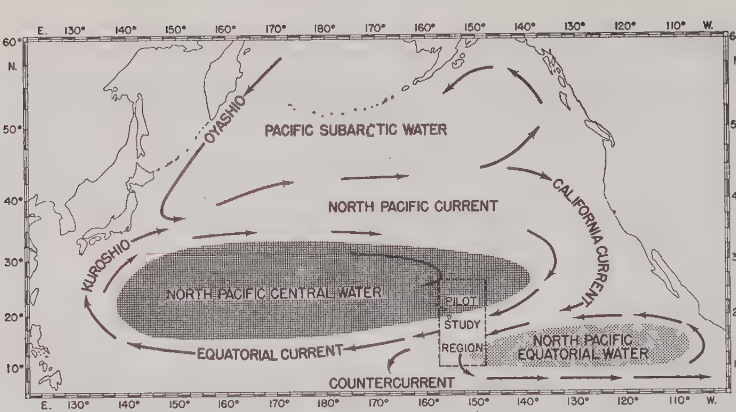
60° N.
50°
40°
30°
20°
10°
E. 130° 140° 150° 160° 170° 180° 170° 160° 150° 140° 130° 120° 110° W.
OYASHIO
PACIFIC SUBARCTIC WATER
NORTH PACIFIC CURRENT
CALIFORNIA CURRENT
KUROSHIO
NORTH PACIFIC CENTRAL WATER
PILOT STUDY REGION
NORTH PACIFIC EQUATORIAL WATER
EQUATORIAL CURRENT
COUNTERCURRENT

Fig. 1. The Trade-Wind Zone Oceanography Pilot Study region with reference to the North Pacific water types and currents.

each station must be adequate to define the boundaries of the water masses. Our previous studies in the central Pacific have shown that vertical sampling at 25-meter intervals in the upper 300 meters along meridional sections separated by 1.5° of latitude is sufficient to delineate the water masses found in the trade-wind zone. The climatic study referred to above [*Seckel,* 1962] indicated that the meridional spacing of stations should be 3° to 5° of longitude.

In the light of these requirements the cruise track and station pattern were laid out as shown in Figure 2. The R. V. *Townsend Cromwell* was able to complete the monthly cruises from February 1964 to July 1965 without exceeding a 20-day limit on each cruise.

On each cruise 43 oceanographic stations were occupied. They were spaced 90 nautical miles (167 km) apart along four meridional sections at 148°, 151°, 154°, and 157°W longitude. Temperature and water samples were obtained at 20 different depths to a depth of 1500 meters at the stations, and bathythermograph observations were made every 0.5° of latitude. Four daily standard marine weather observations were made routinely. The radiation from Sun and sky was measured and recorded daily by an Eppley pyranometer. These measurements were supplemented by cloud photographs in color. On a number of cruises the net long-wave radiation was measured by Suomi-Kuhn radiometer. Biological samples were obtained from surface plankton tows made each evening at 2000 hours. A summary of the observations obtained from the cruises of the pilot study is as follows:

Oceanographic stations (including 33 deep casts)	685
Stations at which oxygen determinations were made	256

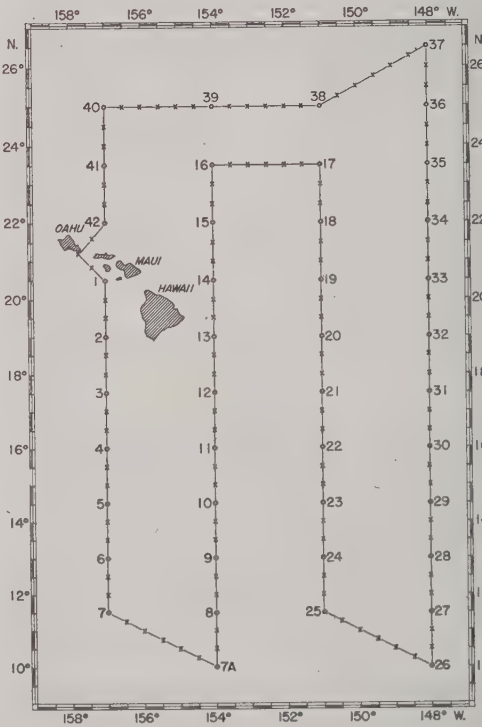
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Fig. 2. Cruise track and station pattern of the Trade-Wind Zone Oceanography Pilot Study. Open dots represent hydrographic stations; crosses represent bathythermograph stations.

Stations at which phosphate determinations were made	162
Bathythermographs	3080
Drift card and bottle releases	29,458
Standard marine weather observations	1280
Pyranometer records (radiation from Sun and sky)	320
Net long-wave radiation measurements	400
Plankton tows	320

The observed oceanographic data together with bathythermograph temperature sections and charts of surface temperature, surface salinity, and surface dynamic heights at the surface relative to 1200 meters have been published [*Charnell et al.*, 1967*a–f*]. Measurements of long-wave radiation from ocean and sky have been reported by *Charnell* [1967].

The Spatial Distribution of Properties

The preliminary analysis of the pilot study data has been concerned with obtaining a description of the distribution of water masses and geostrophic currents. This analysis, although not complete, has yielded interesting examples of the spatial and temporal distributions of the water masses. A part of this material is presented below.

The vertical salinity distribution shown in Figures 3A and B is typical of the North Pacific trade-wind zone (cf. *Reid* [1965], Figure 3) and delineates the principal water masses to be found in the region. These masses are the North Pacific Central Water, the North Pacific Equatorial Water, the North Pacific Intermediate Water, and the Pacific Equatorial Intermediate Water.

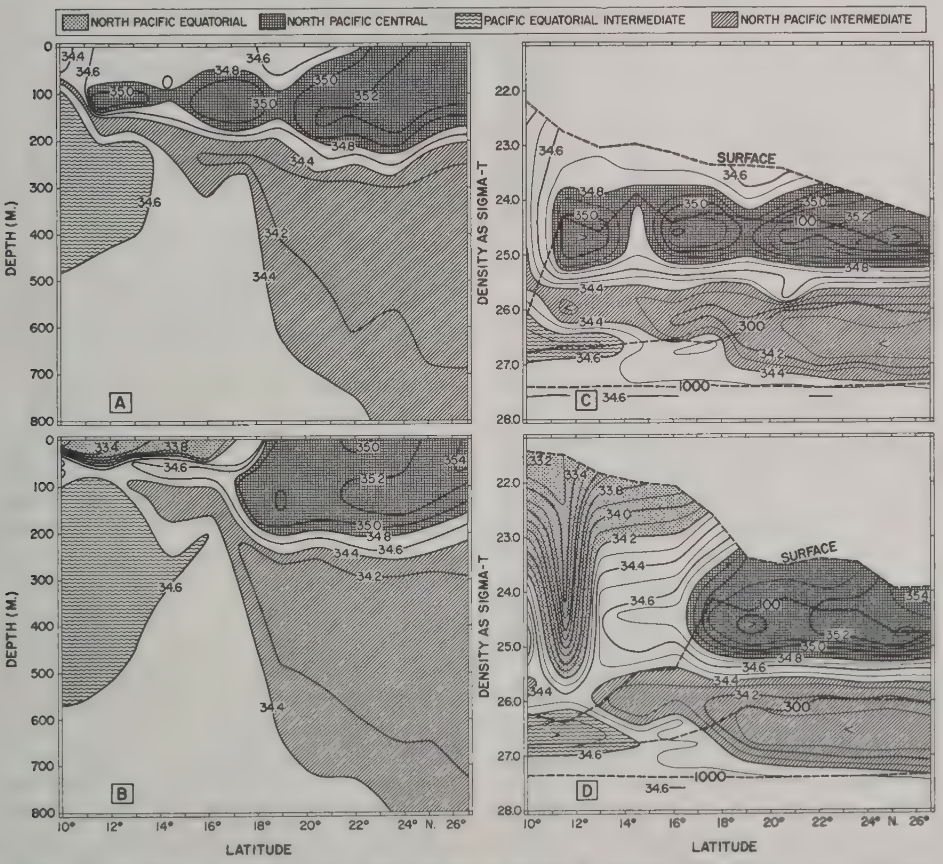

Fig. 3. Meridional salinity (‰) section at 10° to 26.5°N latitude, 148°W longitude. A, latitude-depth, May 1964; B, latitude-depth, October 1964; C, latitude-σ-*t*, May 1964; D, latitude-σ-*t*, October 1964.

The North Pacific Central Water occurs at the surface in the northern portion of the sections and protrudes southward in a tongue below the surface layer (See Figure 3A). It has a salinity of more than 34.8 ‰ and σ-t less than 25.5 (density < 1.0255 at atmospheric pressure).

The North Pacific Equatorial Water has a salinity of less than 34.2 ‰ and σ-t less than 25.5 and occurs as a shallow surface layer in the southern portion of the sections. It is generally found in the eastern Pacific, centered at about 10°N latitude [*Schott,* 1935, Plate XXVII] but may extend westward into the pilot study region, as it did in October 1964.

The North Pacific Intermediate Water, with a salinity of less than 34.4 ‰ and σ-t greater than 25.5, occurs below the North Pacific Central Water in the northern portions of the sections of Figure 3. It markedly decreases in thickness southward of 18°N latitude.

The Pacific Equatorial Intermediate Water has a salinity of more than 34.6 ‰ and σ-t greater than 25.5 and occurs below the North Pacific Equatorial Water in the southern portion of the sections. It has temperature-salinity characteristics that can be found, according to *Reid* [1965], near the surface between latitudes 40° and 50°S and also at intermediate depths in a broad band across the equatorial Pacific.

At the sea surface a relatively high salinity gradient or 'front' near 34.8 to 35.2 ‰ defines the boundary of the North Pacific Central Water. This boundary is seasonally displaced in a north-south direction [*Seckel,* 1962]. These displacements are apparent in the May and October sections (Figures 3A and B), where the boundary is located near latitudes 22° and 18°–19°N, respectively. Similar boundary displacements also occur in the southern portion of the sections. In October a 50-meter deep layer of North Pacific Equatorial Water reaches 17°N latitude; this water had been absent in May.

Relatively high salinity gradients also demark the subsurface boundaries of the North Pacific Central and the North Pacific Intermediate waters. These boundaries may also be temporally displaced. In May the North Pacific Central Water extended subsurface to 11°N latitude and in October only to 17°N latitude, so that the change in location was of the same magnitude as that of the surface boundaries. Boundary displacements of the North Pacific Intermediate Water, although they occur, are less pronounced.

Present evidence indicates that the boundary movements of the North Pacific Central and the North Pacific Equatorial waters were seasonal only at the surface. This was not so for the subsurface boundary of the North Pacific Central Water, although the May and October sections give that impression.

Isentropic analysis in oceanography, particularly as it has been developed by *Montgomery* [1938], has become a powerful method in descriptive oceanography. As a part of this method, characteristic temperature-salinity relationships and associated σ-t values (densities) are used to delineate water masses. If the vertical salinity sections for May and October are redrawn with σ-t as ordinate (Figures 3C and D), the water mass boundaries discussed above become clearly demarked by relatively high salinity gradients. This presentation therefore facilitates water mass identification and the selection of significant σ-t surfaces. In effect, this presentation also expands the upper portion of the ocean and compresses the deeper layers.

The core of the North Pacific Central Water lies at σ-t of about 24.6, and the core of the North Pacific Intermediate Water north of 20°N latitude lies at about σ-t 26.6. South of this latitude this core rises and lies there near σ-t 26.0. Below the shallower tongue of North Pacific Intermediate Water and protruding northward from 10°N latitude, the core of the Pacific Equatorial Intermediate Water lies at σ-t 26.6. Note that the σ-t values of salinity isopleths between the North Pacific Central and North Pacific Intermediate waters are nearly constant. These associations hold true for the whole cruise series. The consistencies testify to the utility of analyzing the distribution of water masses with reference to σ-t surfaces.

In addition to these general features, note the effect of the intrusion of North Pacific Equatorial Water in the October section. It extends downward below σ-t 25.0. Since this layer is only about 50 meters deep, vertical stability is high. This intrusion also means a northward displacement of the subsurface tongue of North Pacific Central Water. At the surface, the intrusion of the North Pacific Equatorial Water and southward displacement of the North Pacific Central Water produced a sharp salinity gradient of roughly 0.5 ‰ per degree of latitude together with a sharp increase in the meridional density gradient between latitudes 16° and 19°N.

The use of σ-*t* rather than depth as ordinate in the vertical sections is deceptive. For example, in October the North Pacific Equatorial Water occupies a large portion of the graph, even though it is only about 50 meters thick; in contrast, the Pacific Equatorial Intermediate Water, centered about σ-*t* 26.6, is several hundred meters thick. This deception has been overcome, in part, by including the 100-, 300-, and 1000-meter isobaths in the sections (Figures 3C and D). These graphs show that the depths of layers vary both with latitude and time. In May, between latitudes 11° and 13°N, Pacific Equatorial Intermediate Water is found below 100 meters, with North Pacific Central and North Pacific Intermediate waters occupying the layers between 100 and 200 meters. In October the latter water masses have been displaced by Pacific Equatorial Intermediate Water, which is within 100 meters of the surface.

The isobaths also show that horizontal density gradients vary from place to place and in depth. In May the rising 100-meter line between latitudes 10° and 12°N indicates a sharp horizontal density gradient without a corresponding feature at 300 meters. The latter isobath shows, however, a relatively high density gradient between 18° and 21°N without a corresponding feature at 100 meters. These relatively high density gradients often mark water mass boundaries. The gradient at 100 meters was at the southern boundary of the North Pacific Central Water; the gradient at 300 meters was related to the change in σ-*t* of the core of the North Pacific Intermediate Water. These associations are also apparent in the October section where, in addition, the sharp density gradient at the sea surface is associated with the transition from North Pacific Central to North Pacific Equatorial Water.

The change in horizontal density gradients with depth and latitude implies complex geostrophic flow; this view is borne out in the meridional velocity sections (Figure 4). The North Pacific Equatorial Current consists of cells of relatively high westerly velocity separated by low-velocity easterly components of flow. Higher velocities (greater than 5 cm sec^{-1}) usually occur in the upper 300 meters.

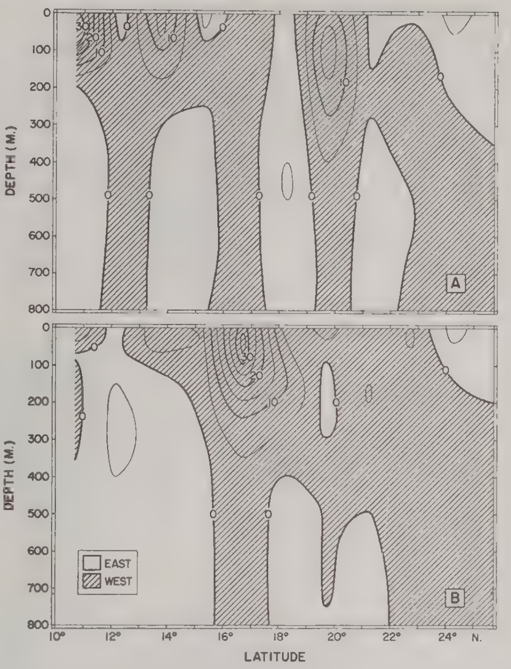

Fig. 4. Meridional section of the east-west component of geostrophic flow (cm sec^{-1}) relative to 1200 meters at 10° to 26.5°N latitude, 148°W longitude. A, May 1964; B, October 1964.

During May there are three dominant cells of westerly flow. The one centered near 11°N latitude is associated with the density gradient at 100 meters, and the cell near 20°N latitude is associated with the density gradient at 300 meters (Figure 3C). In the southern cell the maximum speed is at the surface and is more than 30 cm sec^{-1}. In the northern cell it is below the surface, at approximately 100 meters, and is more than 15 cm sec^{-1}.

During October there is one dominant cell of westerly flow centered about 17°N latitude with a speed of 35 cm sec^{-1} and associated with the density gradients at 100 and 300 meters (Figures 3D) that occur at nearly the same latitude.

Figure 5 summarizes the relation between the water mass distribution and the field of flow. Figure 5A shows the meridional salinity distribution along 148°W longitude for September

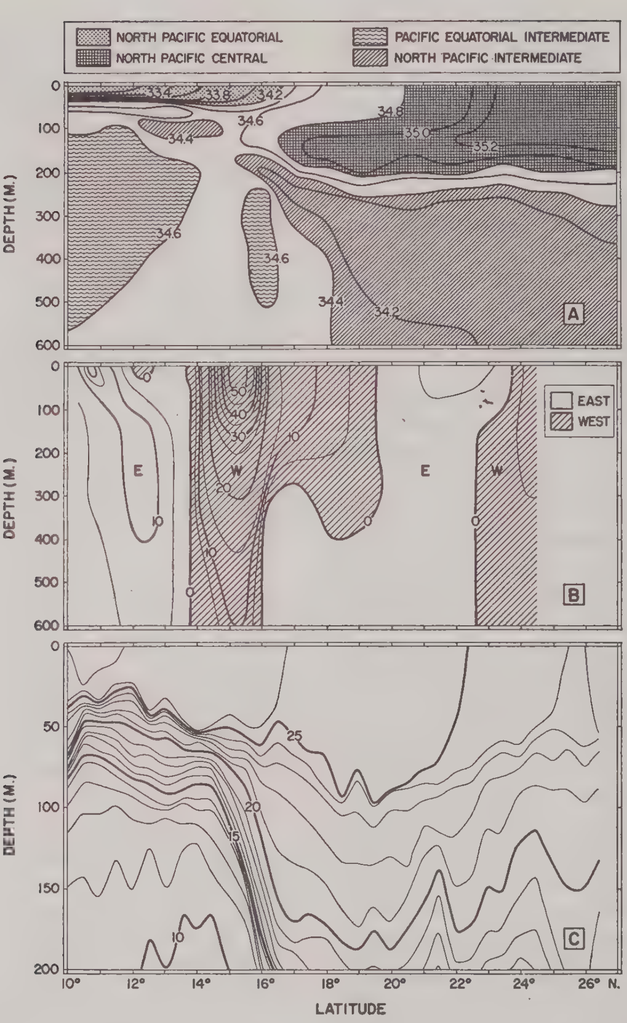

Fig. 5. Meridional sections at 10° to 26.5°N latitude, 148°W longitude, September 1964. A, salinity (‰); B, east-west components of geostrophic flow (cm sec^{-1}) relative to 1200 meters; C, bathythermograph temperatures (°C).

1964. Figure 5B shows the east-west components of geostrophic flow for the same section. The North Equatorial Current, present in a single cell of high westerly flow, is associated with the water mass boundaries shown in the upper panel. Figure 5C, with an expanded depth scale, shows the meridional temperature distribution; here the pronounced feature is a thermal front of approximately 5°C per degree of latitude below 70 meters near latitudes 15° and 16°N, corresponding to the water mass boundary and the cell of high geostrophic flow.

The Temporal Distribution of Properties

The pilot study has not progressed sufficiently to determine mass and volume budgets. The nature of the time changes in the distribution of properties is, however, apparent.

The surface temperature, surface salinity, and the east-west component of the surface geostrophic flow from February 1964 to June 1965 are shown in Figure 6. The slope of the isopleths signifies latitudinal displacements from month to month. The seasonal north-south displacement of isotherms in response to the annual cycle of net heat exchange across the sea surface (Figure 6A) is so pronounced that it tends to obscure other processes, such as advection, that also affect the distribution of the surface temperature [*Seckel*, 1962]. The irregularity of the temperature pattern indicates, however, that the net heat exchange across the sea surface is not the only factor involved. For example, the surface temperature declines at more than 1°C per month from October to November in both the northern and southern portions of the section and again from January to February between latitudes 19° and 22°N. On the basis of our present knowledge, these changes are more than those expected from the net heat loss at the sea surface.

The surface salinity indicates changes in the

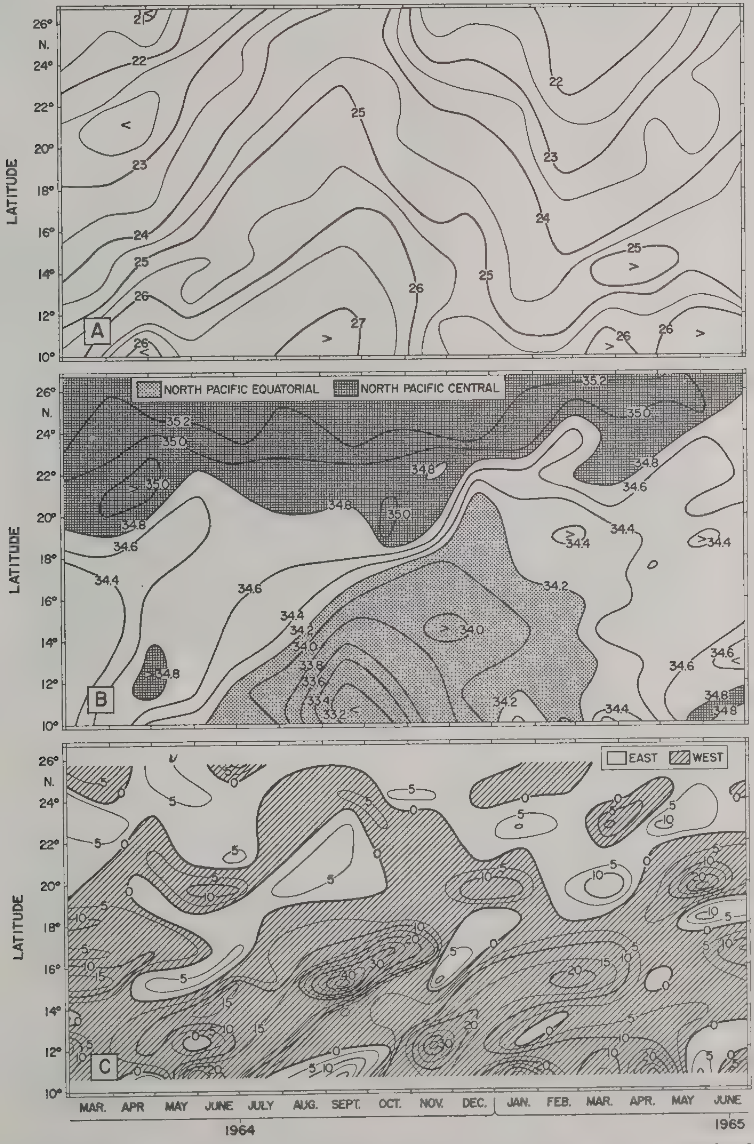

Fig. 6. Distribution at the sea surface, 10° to 26.5°N latitude, 148°W longitude, February 1964 to June 1965. A, temperature (°C); B, salinity (‰); C, east-west component of surface geostrophic flow (cm sec^{-1}) relative to 1200 meters.

distribution of water types (see Figure 6B). The pilot study period saw a general northward displacement of the North Pacific Central Water upon which the seasonal displacements were superimposed. The northward displacement reached 22°N latitude in June 1964 and 25° to 26°N latitude in June 1965.

The intrusion of North Pacific Equatorial Water forms a pronounced feature in the salinity section. It began in June 1964, reached 21°N latitude in December, and thereafter rapidly disappeared. Figure 6B also shows the dilation and concentration of the transition zone (the California Current extension) that result from the seasonal displacements of the North Pacific Central and North Pacific Equatorial waters.

Figure 6C shows the distribution of the easterly and westerly components of geostrophic flow. South of 19°S latitude, easterly components of flow are present within the generally westward flowing North Pacific Equatorial Current. At 10°N latitude the easterly component of flow between July and October may mean northward displacement of the Equatorial Countercurrent. The cell of high westerly flow shown in Figures 4 and 5 is apparent at approximately 15° to 17°N latitude during September and October.

North of 19°N latitude is a continuous band of easterly flow (Figure 6C). This band is located between latitudes 20° and 25°N in February and is displaced toward 26°N latitude during July to September. After this time the band persists at various latitudes north of 18°N. Continuous bands of easterly flow are also found at about the same latitude range in similar charts for longitudes 151°, 154°, and 157°W. This feature appears, therefore, to be continuous in time and space and thus may be used to define the northern boundary of the North Pacific Equatorial Current. Currents are variable to the north of the continuous band of easterly flow.

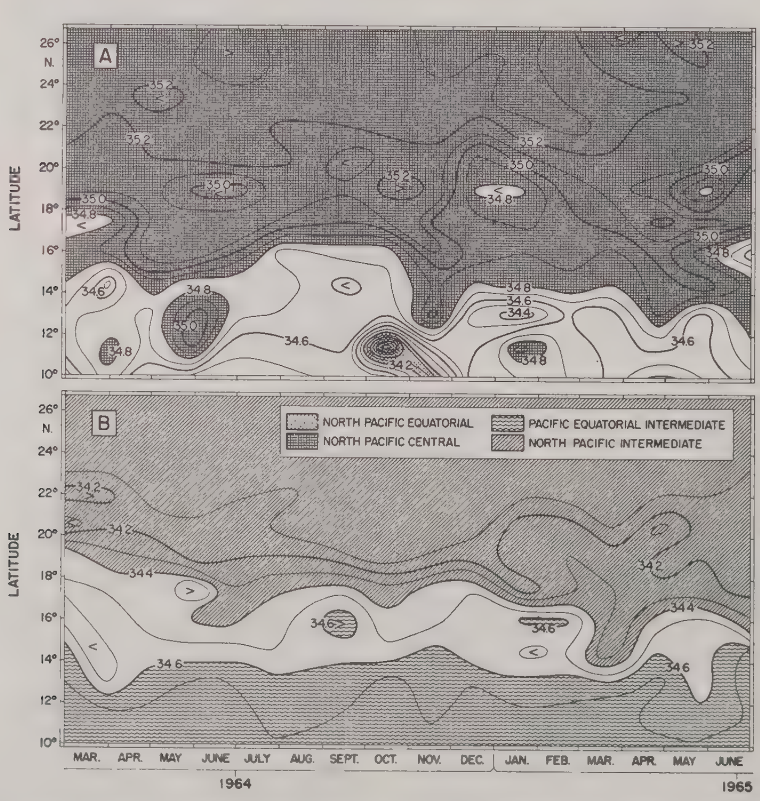

Fig. 7. Distribution of salinity (‰) at 10° to 26.5°N latitude and 148°W longitude, February 1964 to June 1965. A, on the σ-t 24.6 surface; B, on the σ-t 26.6 surface.

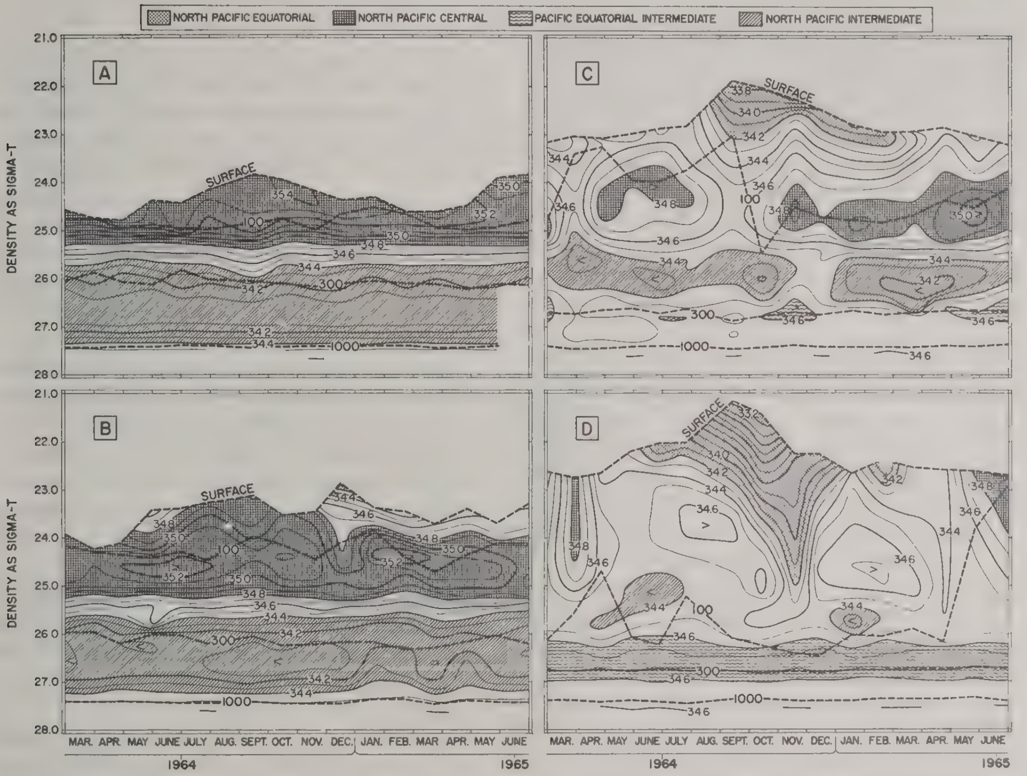

Fig. 8. Vertical profile of salinity (‰) February 1964 to June 1965. A, station at 26.5°N latitude, 148°W longtitude; B, station at 20.5°N latitude, 148°W longtitude; C, station at 14.5°N latitude, 148°W longitude; D, station at 10°N latitude, 148°W longitude.

Figures 7A and B show the distribution of salinity on the *σ-t* 24.6 surface (the high-salinity layer) and on the *σ-t* 26.6 surface (the low-salinity layer). In Figure 7A the relatively high salinity gradient, which indicates the boundary of the North Pacific Central Water, is generally well-defined and fluctuates between latitudes 13° and 19°N. No seasonal variation in the latitude of the water mass boundary is apparent, although intrusion of lower salinity water in the southern portion between September and November is probably seasonal.

In Figure 7B the relatively high salinity gradient along the water mass boundary of the North Pacific Intermediate Water is also well-defined. It lies between latitudes 13° and 20°N. Although the boundary shows less latitudinal fluctuation than the North Pacific Central Water boundary shown in 7A, individual salinity isopleths indicate possible displacements of more than a degree of latitude per month. Again, no seasonal variation in the latitude of the boundary is indicated.

Figures 6B, 7A, and 7B show the areal distribution of the characteristic water masses and their boundaries in the trade-wind zone. Like the boundaries of air masses, water mass boundaries fall within specific geographic limits and may fluctuate seasonally, on a longer term basis, and randomly.

The vertical distribution of water masses at individual stations from February 1964 to June 1965 is presented in Figure 8. At 26.5°N latitude (Figure 8A), the North Pacific Central water forms the surface layer throughout the year. Variations are mostly confined to the seasonal change in surface temperature. Below this layer, in the transition to the North Pacific Intermediate Water, and in the deeper portion of the salinity minimum layer, the salinity *σ-t* relation remains remarkably stable throughout the cruise series.

Conditions change as one progresses southward to 20.5°N latitude, where the North Pacific Central Water is at the surface only during the brief periods from March to May 1964 and October and November 1964 (Figure 8B). During the other months a lower salinity surface layer is present. Although the transition layer between the North Pacific Central Water and North Pacific Intermediate Water remains at essentially the same σ-t values throughout the period, the salinity in the minimum layer begins to vary.

Farther south, the station at 14.5°N latitude lies within the boundary region of the three layers under consideration (see Figure 8C). At the surface, North Pacific Equatorial Water is present from August 1964 to March 1965. Below the surface, the North Pacific Central Water and the North Pacific Intermediate Water are no longer present throughout the year, and Pacific Equatorial Intermediate Water is present at σ-t 26.6 during February and March, November and December, 1964, and May to July 1965.

At 10°N latitude North Pacific Equatorial Water forms the dominant feature from June 1964 until March 1965 (Figure 8D). The deeper North Pacific Intermediate Water has been replaced by Pacific Equatorial Intermediate Water, which is present throughout the pilot study period. Two cells of shallow North Pacific Intermediate Water are present from May to July 1964 and January and February 1965. Evidence of the proximity of North Pacific Central Water, although of lower salinity, is present in two cells during July to October 1964 and January to April 1965. Cells of high-salinity water appear at the surface in March and April 1964 and June 1965. They are not believed to be of the North Pacific Central type.

Each station has its characteristic 'oceanographic climate.' At 26.5°N latitude, a distance from the water mass boundaries, changes are principally confined to the surface layer and reflect the effects of the annual cycle of processes at the sea surface, such as the net heat exchange. Within the water mass boundary region, changes are pronounced and reflect seasonal processes at the sea surface that affect the surface layer directly and reflect boundary meanders and eddy formations that arise from other mechanisms.

Concluding Remarks

The trade winds form the largest and most persistent wind system and the principal atmosphere-to-ocean energy transfer system, affecting all parts of the ocean. In this zone the North Pacific Equatorial, North Pacific Central, North Pacific Intermediate, and Pacific Equatorial Intermediate water masses are found, within 300 meters of the surface, to have temperature-salinity characteristics that occur near the ocean surface between latitudes 40°N and 40°S.

The boundaries of these major water masses lie within this zone and are intimately related with the field of geostrophic flow. The presence of the boundaries means that the trade-wind zone is a region where the transfer of dissolved substances from one water mass to another takes place and where, by mixing, new water masses can be formed.

These characteristics are of significance in ecological studies, in the exploration and harvest of fishery resources, in determination of acoustic properties, and in the solution of possible radioactive pollution problems.

Because of the significance of the trade-wind zone characteristics, the Trade-Wind Zone Oceanography Pilot Study will form the basis of more extensive investigations into the processes that take place in this portion of the world's oceans.

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ABSTRACT

FARMING OYSTERS IN ARTIFICIAL PONDS — ITS PROBLEMS AND POSSIBILITIES

William N. Shaw

U. S. Bureau of Commercial Fisheries
Biological Laboratory
Oxford, Maryland

Four 1/4-acre artificial saltwater ponds were put into operation in the fall of 1964 at Oxford, Maryland. Three oyster culture studies were initiated in the ponds: production of seed oysters; comparative growth of 7 strains of Chesapeake Bay oysters, and response of oysters to 4 types of bottom. In addition, a 2-year ecological study was made of the invertebrate succession and pond colonization.

About 10 spat per 30 shells were caught in the first attempt to produce seed oysters in an artificial pond. The seed originated from the introduction of 4 to 5 million straight-hinged larvae (48 hours old). In the comparative growth study, all strains grew at about the same rate, but meat quality was lower than in similar groups suspended in a natural pond. Condition of oysters (percentage of solids) declined on all 4 types of bottom from an apparent lack of food; thus the effect of bottom type was overshadowed by other factors.

Future studies will refine methods of producing seed oysters, and develop methods of feeding pond-held oysters. We believe that artificial ponds have a commercial potential for culturing oysters which will be determined by further biological research.

Some Effects Of Logging On Two Salmon Streams In Alaska

William L. Sheridan and William J. McNeil

Science

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THE AUTHORS: Sheridan is regional fishery biologist, Forest Service Alaska Region in Juneau, Alaska; McNeil, formerly with the Bureau of Commercial Fisheries, Auke Bay Laboratory, Juneau, is now with Oregon State University, Department of Fisheries and Wildlife, Newport.

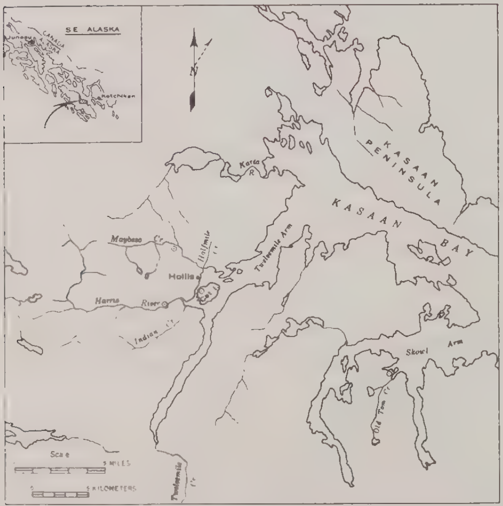

Fig. 1.—Location of Harris River and Twelvemile Creek on Prince of Wales Island, southeastern Alaska.

ABSTRACT. — Sedimentation of spawning beds and density of pink salmon (Oncorhynchus gorbuscha) *were observed before and after logging in two streams in southeastern Alaska. The study lasted seven years (1958-1964). Although the amount of fine particles in spawning beds increased temporarily, the amount in 1964 (five years after logging began) was not significantly greater than in 1959. Densities of salmon spawners and fry increased in the sampling areas during the period of this study. The increases were probably due to the abolition in 1959 of salmon traps (formerly the primary means of catching salmon).*

THE OPERATION of pulp mills at Ketchikan since 1954 and at Sitka since 1960 has caused rapid expansion of logging in southeastern Alaska. Watersheds of the more important spawning streams of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southeastern Alaska will eventually be logged.

Successful reproduction of pink and chum salmon requires streams with gravel beds that do not contain excessive quantities of fine particles. Pink and chum salmon commonly spawn in southeastern Alaska streams in August and September and bury their eggs 10 to 30 cm deep in the gravel. The eggs hatch in November and December, and the young salmon emerge from gravel beds in March, April, and May when they migrate immediately to sea. Survival of embryos and alevins (young salmon between the time they hatch from the egg and emerge from the streambed) is sometimes reduced because fine particles in the streambed restrict the flow of oxygen-bearing water.

To evaluate effects of logging on salmon spawning streams, the Alaska Forest Research Center (now Institute of Northern Forestry) initiated studies in 1949 on water temperature, stream discharge, settleable solids in stream water, and wood debris in stream channels. Studies of the effects of logging were expanded in 1956 when the U. S. Bureau of Commercial Fisheries gave a contract to the Fisheries Research Institute, University of Washington for evaluating the effects of specific environmental factors on survival of pink salmon eggs and alevins. The effects of logging on spawning beds of pink salmon were studied by personnel of the Fisheries Research Institute in Harris River and Twelvemile Creek 40 miles west of Ketchikan (near Hollis) on the east shore of Prince of Wales Island (Fig. 1).

Information on fine particles in spawning beds and density of salmon was obtained before, during, and after logging. Fine particles were measured in spawning beds from 1959 through 1964, and pink salmon spawners and their resultant progeny were counted from 1958 through 1964. These measurements and counts are evaluated here.

Description of Streams and Watersheds

Area of the Harris River watershed is 83 km², 22 percent of which was logged during the present study. The only previous logging on this watershed involved selective removal of a few trees for construction of aircraft in World War I and for mining activities.

Pink and chum salmon spawn in the intertidal zone of Harris River and upstream as far as 13 km. Width of spawning beds varies between 10 and 35 m. Average gradient of the intertidal zone and the first 5 km segment of streambed above mean high tide is 0.30 percent. Stream discharge fluctuates widely during the spawning period, late August and September, but is usually between 22 and 1800 cubic feet per second (cfs). During fall storms, discharge may average 5,000 cfs over any 24-hour period.

Area of the Twelvemile Creek watershed is 36 km² 29 percent of which was logged during the study. Previously some trees were selectively harvested for aircraft in World War II.

About 8 km of stream are accessible to salmon, and spawners were normally most dense in the upper intertidal zone. Width of spawning beds varies between 6 and 18 m. Average gradient of the intertidal zone and the first 2-km segment of streambed above mean high tide is 0.12 percent. Stream discharge during the spawning period fluctuates widely, but is mostly between 12 and 600 cfs. During fall storms, discharge may average 1,000 cfs. over a 24-hour period.

Account of Logging

Road construction and logging began on the Harris River watershed in 1957 and ended in 1962. To harvest the timber over 37 km of roads had been constructed by 1960. Annual extent of harvest, mostly obtained by cable logging, is given in Table 1.

Road construction and logging began on the Twelvemile Creek watershed in 1959 and continued into 1964 when this study ended. At least 20 km of roads had been constructed by 1964. Annual extent of harvest, obtained by cable and tractor logging, is given in Table 2.

Species composition of the harvestable timber in both watersheds was about 70 percent western hemlock (*Tsuga heterophylla*), 25 percent Sitka spruce (*Picea sitchensis*) and 5 percent western redcedar (*Thuja plicata*). Areas were clearcut in patches as is customary in southeastern Alaska (Fig. 2).

Sedimentation

Deposition of fine particles in spawning beds was evaluated in sampling areas by periodic measurements of size composition of streambed materials. Three sampling areas were established in Harris River and two in Twelvemile Creek—the areas are described in Table 3.

Samples of bed materials were collected at random locations (established by use of tables of random numbers) in each sampling area, and analyzed for size composition as done by McNeil and Ahnell (*9*). Twenty-five points were intended for inclusion in each sample; this number was occasionally reduced by 1 to 5 points through errors in collection or measurement. Each point was a core of streambed 10.2 cm diameter and 15.2 cm deep. The materials were sieved wet through a graded series of nine Tyler sieves with

Table 1.—Progress of Logging in the Harris River Watershed, 1957-1962

Year	Area logged	Cumulative area logged
	hectares[1]	*hectares*
1957	84.6	84.6
1958	0	84.6
1959	673.8	758.4
1960	550.8	1309.2
1961	483.6	1792.8
1962	59.9	1852.7

[1] One hectare = 2.47 acres, or 0.01 sq. km.

Table 2.—Progress of Logging on Twelvemile Creek Watersheds, 1959-1964

Year	Area logged	Cumulative area logged
	hectares	*hectares*
1959	31.6	31.6
1960	181.3	212.9
1961	205.6	418.5
1962	115.3	533.8
1963	346.4	880.2
1964	155.0	1035.2

Table 3.—Location and Size of Sampling Areas, Harris River and Twelvemile Creek

Stream and area	Location	Size (m²)
Harris River		
Intertidal	4.0 to 4.3 meters elevation above zero tide elevation	4,144
Upstream Area A	0.8 km upstream from mean high tide elevation[1]	4,327
Upstream Area B	1.5 km upstream from mean high tide elevation[1]	7,178
Twelvemile Creek		
Intertidal	3.7 to 4.7 meters elevation above zero tide elevation	5,678
Upstream	1.0 km upstream from mean high tide elevation[1]	3,666

[1] Mean high tide elevation at Hollis is about 4.3 meters above zero tide elevation.

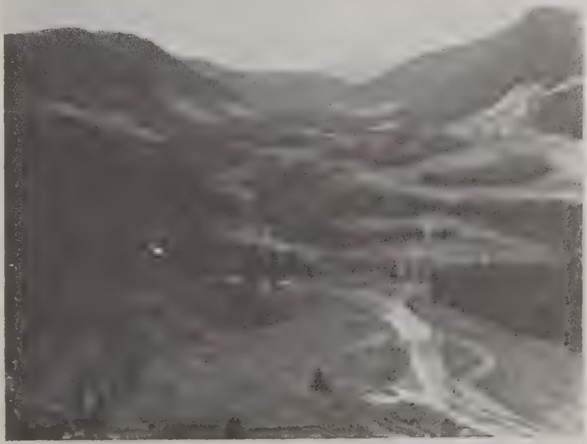

Fig. 2.—Portion of the Harris River watershed showing typical clearcut areas. The intertidal zone appears in the right foreground.

openings from 26.26 to 0.104 mm. Water and materials in suspension which passed the finest sieve were collected and placed in a settling funnel. Solids were allowed to settle in the funnel for 10 minutes before discarding of the supernatant liquid. Because the diameter of the opening of the sampler was 10.2 cm, rocks of larger diameter were excluded. The volume of material retained by each sieve and settling from suspension in the funnel was expressed as a percentage of the total volume of the sample.

The first samples were collected in 1959 and the last in 1964. Relatively little logging had occurred upstream from the sampling areas before 1959. Samples were collected at various times of the year, but mostly in summer.

Sediment in Harris River.—Sampling was done in summer, fall, and winter of 1959 and 1960 to define seasonal variations in amount of fine particles in spawning gravels. Materials less than 0.833 mm are designated as fine particles. Experiments have established that presence of fine particles causes a significant reduction in permeability of salmon spawning beds (*3,9*). Estimates of percentage of fine particles in the total volume of gravel in the sampling areas are given in Table 4.

The volume of fine particles in spawning beds fluctuated between summer and fall and fall and winter. The intertidal area contained smaller amounts of fine particles in October than in August 1959 and 1960. No difference appeared in upstream Area A between August and October 1959; but in upstream area B the amount of fine particles increased between August and October 1959, and decreased between October 1959 and February 1960.

Processes that cause changes in the quantity of fine particles in the spawning beds of Harris River were discussed by McNeil and Ahnell (*9*), who concluded that an abundance of spawners in September 1959 and 1960 caused removal of fine particles from the intertidal area. Cooper (*3*), also described this occurrence in streams in British Columbia. Scarcity of spawning salmon in the upstream areas may have been the reason that fine particles were not removed there.

An increase in the volume of fine particles in upstream area B from August to October 1959 was attributed by McNeil and Ahnell (*9*) to sedimentation from logging and the subsequent decrease in February 1960 was attributed to flooding. They stated:

> Land areas contiguous to the upstream sampling area of Harris River were logged in late summer and autumn 1959. From personal observation, it was apparent that tributary streams draining the logged areas carried unusually heavy silt loads during freshets. Water samples collected from three tributary streams during freshets contained, on the average, two to four times more inorganic sediment after logging than before. The average amount of organic sediment in samples collected after logging was only fractionally more than the amount in samples collected before logging. Because of the high variability observed in the amount of sediment carried by the tributary streams and the small numbers of samples collected, it is not possible to show conclusively that the content of inorganic sediment increased because of logging. However, the data . . . lend support to this conclusion.
>
> Bottom samples obtained from upstream in Harris River in August and October 1959 revealed that the volume of silts and fine sands in spawning beds increased significantly during periods when tributary streams appeared to carry increased amounts of inorganic sediments. Similar increases did not occur in intertidal Harris River, suggesting that settleable solids were not transported downstream in significant amounts, or in Indian Creek (a tributary to Harris River), which was unlogged. Instead, the volume of fine particles in intertidal Harris River and Indian Creek declined significantly between late summer and mid-autumn, possibly because of spawning activity.
>
> The deposition of fine materials in the upstream Harris River sampling area was found to be temporary. Flooding occurred in the periods November 5-7 (5.32 inches of rain in 72 hours) and December 5-7 (7.02 inches of rain in 72 hours). In samples of bottom materials obtained from upstream Harris River after flooding (February 23, 1960), the content of fine materials had returned to the level observed in summer 1959 before logging.

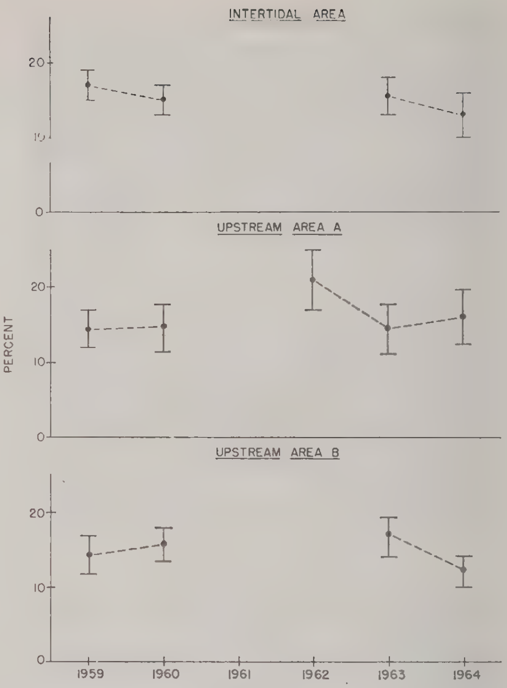

Fig. 3.—Percentage of particles <0.83 mm in the total volume of gravel in Harris River sampling areas; August 1959 through 1964. Dots represent sample means and vertical bars the 95 percent limits of mean values.

Because the amount of fine particles in the Harris River streambed changed seasonally, long term changes were evaluated from samples collected during summer. The data are shown in Figure 3 for the three

Table 4.—Percentage of Fine Particles in the Total Volume of Gravel in Harris River Sampling Areas, August and October 1959 and February, August, and October 1960

Area and month	Percentage of total volume of streambed materials <0.833 mm: Mean	95 percent confidence limits of mean
Intertidal Area		
August 1959	16.7	±1.8
October 1959[1]	12.8	±1.4
October 1959[1]	13.8	±2.1
August 1960	14.7	±2.1
October 1960	11.6	±1.6
Upstream Area A		
August 1959	14.0	±2.2
October 1959	14.2	±2.1
Upstream Area B		
August 1959	13.9	±2.1
October 1959	17.5	±2.5
February 1960	14.1	±1.3

[1] Sampling was replicated.

sampling areas. The values for 1964 did not differ significantly from those for 1959 (pre-logging sample) in upstream areas A and B; hence, increased volumes of fine particles in the upstream areas were transitory and their effects lasted less than 5 years. Volume of fine particles in the intertidal area appeared to decline over the period of observation.

Increased volume of fine particles in the upstream Harris River sampling area between August 1960 and August 1962 may have resulted from landslides which occurred on the watershed in October 1961 upstream from both areas A and B. The increase in the amount of fine particles from August 1960 to August 1962 was significant at the 1 percent level for upstream area A. Because no samples were collected, it was not determined if a similar increase occurred in upstream area B. Volume of fine particles had returned to the pre-logging level in upstream area A by the summer of 1963. Sample means of the percentage of fine particles in the total volume of gravel in upstream area A before and after the landslides in 1961 were as follows:

August	1960	14.4	percent
....	landslides in	1961	.. ....
August	1962	20.9	percent
June	1963	14.1	percent

Table 5.—Percentage of Fine Particles in the Total Volume of Gravel in the Intertidal Zone Sampling Areas of Twelvemile Creek, August and November 1960

Time	Percentage of total volume of streambed materials <0.833 mm: Mean	95 percent confidence limits of mean
August 1960	18.8	±1.9
November 1960	15.7	±2.4

The landslides occurred in cutover areas; possibly they would not have occurred if the Harris River watershed had not been logged. Bishop and Stevens (*1*) concluded that logging contributed to landslides on steep slopes of watersheds in southeastern Alaska after heavy rainfall. Landslides on the Harris River watershed occurred in October and November 1961 after very heavy rainfall. On October 13, for example, 5 inches of rain fell at Hollis in 24 hours; such a heavy rainfall is expected once in 10 years. Total precipitation for October 1961 was 32.2 inches, 10 inches above the long term average.

Sediment in Twelvemile Creek.—Samples in August and November 1960 (Table 5) suggested that fine particles decreased in the intertidal area of Twelvemile Creek in summer or fall much as in the intertidal area in Harris River (Table 4). The decrease in fine particles could have been caused by salmon spawning in September.

Removal of gravel from a pit about 5 km upstream from the study areas may have contributed to the relatively large volume (18.8 percent) of fine particles in the streambed in August 1960. This removal was the source of heavy sediment carried by a small tributary and discharged into Twelvemile Creek. Turbid water extended into the bay 4 km downstream. Suspended solids were measured in the tributary and mainstream June 22, 1960, to estimate the amount of solids deposited (Table 6).

The tributary carried almost 912 kg of suspended solids per hour into the mainstream. Upstream from the tributary, Twelvemile Creek was clear; 370 m downstream from the confluence, the stream carried about 319 kg of suspended solids per hour; and 5 km downstream, the load was 274 kg per hour.

Table 6.—Concentrations of Suspended Sediment (parts per million), Twelvemile Creek and Tributary, June 1960

Location of sampling	Sample 1	2	3	4	5	6	Ave.
In tributary	3,251	1,397	1,577	1,663	1,383	1,561	1,805
In Twelvemile Creek							
30 m upstream from tributary's confluence	0	0	0	0	1.4	0	0.23
370 m downstream from tributary's confluence	52	42	50	46	43	34	45
5 km downstream from tributary's confluence	36	38	39	41	40	40	39

Table 7.—Estimated Density of Female Pink Salmon Spawners in Sampling Areas of the Harris River, 1958-1964

	Number of females per m²						
Sampling area	1958	1959	1960	1961	1962	1963	1964
Intertidal	0.10	0.26	0.50	0.73	3.34	0.47	0.37
Upstream (A&B combined)	0.02	0.06	0.03	0.19	0.79	0.18	0.40

Because of variations in the amount of fine particles in the streambed within a year, annual trends in the amount of fine particles in the sampling areas were evaluated from samples collected only during summer (Fig. 4). As in Harris River, increased volumes of fine particles lasted less than 5 years. (Estimates for 1964 did not differ significantly from those for 1959.) By 1964, logging in the Twelvemile Creek watershed was remote from the sampling areas.

Density of Salmon

The density of pink salmon spawners and alevins was estimated in the sampling areas to determine major changes in levels of production. The density of spawners was estimated in late August and September 1958-1964, and the density of alevins in late winter or early spring 1958-1965.

To estimate the number of female spawners, the study areas were censused daily. Total number of females spawning in each study area was estimated by the following method:

$$\text{Number spawning} = \frac{\Sigma \text{ daily counts of females}}{\text{Average redd life of females}}$$

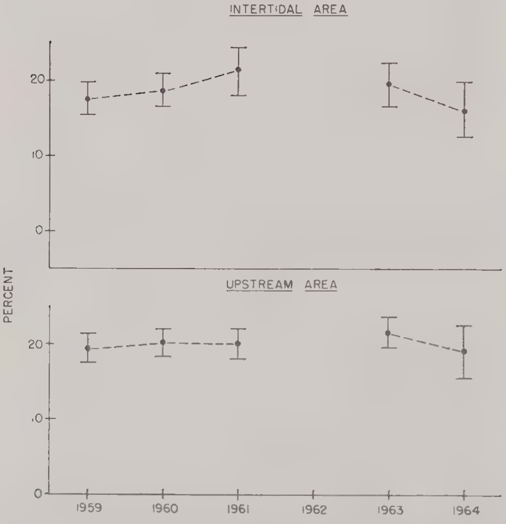

Fig. 4.—Percentage of particles <0.83 mm in the total volume of gravel in Twelvemile Creek sampling areas; August 1959 through 1964. Dots represent sample means and vertical bars the 95 percent confidence limits of mean values.

Daily counts were summed by fitting a curve to the number of females counted each date a census was made and determining the area under the curve. Average redd life (days on the spawning ground) was determined from daily observations on tagged females. The method was described more fully by McNeil (*6,7*). Results of a recent study (*8*) suggested that the method provides realistic estimates of actual numbers spawning. Density is calculated by dividing the number of females estimated to spawn by the area of spawning bed (m²).

Alevins in the spawning gravel were sampled in late winter or early spring. Fry emerged shortly after the samples had been collected. Collections were made from enclosed quadrates or circles of streambed (sampling units) of known size (0.2 to 0.4m²) with a hydraulic sampler (*6*). The standard number of samples was 50, although from 1958-60 more samples were sometimes obtained. Sampling units were located randomly within the study areas by use of tables of random numbers. Separate estimates of density of live alevins were made for intertidal Harris River, upstream Harris River (areas A and B combined), and intertidal Twelvemile Creek.

Density of salmon in Harris River.—Densities of salmon were higher in the intertidal than in upstream study areas of Harris River. The intertidal area had the highest density of spawners every year but 1964 (Table 7), and the highest density of alevins in all years (Table 8). The abundance of female pink

Table 8.—Estimated Density of Pink Salmon Alevins in Sampling Areas of the Harris River, 1958-1965

	Number of live alevins per m²	
Sampling area and year	Mean	90 percent confidence limits of mean
Intertidal		
1958	12	±13
1959	107	±82
1960	123	±49
1961	71	±30
1962	82	±66
1963	168	±52
1964	116	±47
1965	203	±98
Upstream (Area A and B combined)		
1958	no estimate	—
1959	6	± 6
1960	0	–
1961	no estimate	
1962	no estimate	
1963	82	±82
1964	17	±19
1965	48	±49

Table 9.—Estimated Density of Pink Salmon Spawners in Sampling Areas of Twelvemile Creek, 1958-1964

Sampling area	Number of females per m² in year						
	1958	1959	1960	1961	1962	1963	1964
Intertidal	0.11	0.15	0.25	0.28	0.60	0.48	0.69
Upstream	0.01	0.01	0.10	0.08	no est.	0.44	0.76

salmon spawners and alevins tended to increase after 1958. Possible reasons for this trend are discussed later.

Density of salmon in Twelvemile Creek.—As in Harris River, female spawners were more abundant in Twelvemile Creek in the intertidal than in the upstream area and density trended upward after 1958 (Table 9). Density of alevins was studied only in intertidal Twelvemile Creek (Table 10). There was an increasing trend in density over the period of observation similarly to that in the Harris River.

Sedimentation and Reproduction of Salmon

It is well known that fine particles are detrimental to embryos and alevins of salmon. Where amounts of fine particles in spawning beds are excessive, the rate of water flow through the streambed is reduced and the quality of water bathing salmon embryos and alevins is impaired (*2,3,4*). Fine particles may be detrimental also if they adhere to the chorion of eggs (*10*), or impede the emergence of fry (*5*).

Natural factors that remove fine particles from spawning beds include spawning of salmon and flooding. Presence of fine particles in spawning beds is more likely to be long lasting in streams with relatively stable flows or a scarcity of spawners than in streams with periodic flooding or an abundance of spawners.

Deposition of fine particles in upstream spawning beds of the Harris River possibly resulted from road construction and from landslides, but was temporary. Deposition of fine particles in spawning beds of Twelvemile Creek possibly resulted from road construction and was also temporary. By summer 1964, no increase could be demonstrated in the amounts of fine particles in spawning beds above the pre-logging levels of 1959.

The escapement of pink salmon spawners and production of alevins exhibited an upward trend in both study streams after 1958. This rise which was during the period of logging, probably was due to the abolition of salmon traps in 1959. Before 1959, salmon traps accounted for the major portion of salmon caught in southeastern Alaska. The rate of exploitation of the Harris River and Twelvemile Creek stocks of pink salmon may have been reduced enough in 1959 and later years to allow for increased escapement of adults and increased production of alevins.

Table 10.—Estimated Density of Pink Salmon Alevins in Intertidal Sampling Area of Twelvemile Creek, 1958-1965

Year	Number of live alevins per m²	
	Mean	90 percent confidence limits of mean
1958	No estimate	
1959	1	± 2
1960	< 1	± 1
1961	47	±30
1962	No estimate	
1963	57	±26
1964	23	±23
1965	74	±67

The effect of deposition of fine particles in salmon spawning beds on production of pink salmon is receiving additional evaluation. The Alaska Department of Fish and Game and the U. S. Forest Service are using methods developed by the Fisheries Research Institute at Hollis to monitor other pink and chum salmon spawning streams where watersheds will soon be logged. The U. S. Bureau of Commercial Fisheries provides supporting funds for this monitoring program.

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The Fisheries Research Institute of the University of Washington made data available on which part of this report is based. The South Tongass National Forest furnished information on the history of logging in the Harris River and Twelvemile Creek watersheds. The Auke Bay Biological Laboratory of the Bureau of Commercial Fisheries, the Institute of Northern Forestry Research, the Fisheries Research Institute, and the Regional Office of the Alaska Region of the Forest Service offered helpful criticism of the manuscript. ☐

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OBSERVATIONS ON THE DISTRIBUTION AND BREEDING OF *SAGITTA ELEGANS* (CHAETOGNATHA) IN COASTAL WATERS OF THE GULF OF MAINE

By Kenneth Sherman and Everett G. Schaner

OBSERVATIONS ON THE DISTRIBUTION AND BREEDING OF *SAGITTA ELEGANS* (CHAETOGNATHA) IN COASTAL WATERS OF THE GULF OF MAINE

Kenneth Sherman and Everett G. Schaner
Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine 04575

ABSTRACT

The chaetognath *Sagitta elegans* Verrill in the coastal waters of the Gulf of Maine undergoes seasonal fluctuations in abundance, progressing from a spring low to a summer high and declining in fall and winter. These fluctuations are related to the breeding cycle; one generation of S. *elegans* is produced annually. Breeding extends from spring through fall; maturing specimens dominate in winter and immature specimens in summer. Death of mature individuals after breeding appears to cause the spring population decline. Areal differences in abundance are influenced by the dominant nontidal drift, which moves southwesterly along the Maine coast. In winter, when the drift is poorly developed, S. *elegans* is evenly distributed along the coast. Numbers increase progressively westward in summer and fall with the development of nontidal drift; they reach an annual peak in the western area (Cape Elizabeth, Maine, to Cape Ann, Massachusetts) during fall. Concentrations of S. *elegans* along the coast are apparently the result of local breeding. There is no evidence of large-scale transport of S. *elegans* to local areas from other breeding centers in the Gulf of Maine.

INTRODUCTION

The zooplankton in coastal waters of the Gulf of Maine was sampled from 1963 to 1966 as part of a research program on stocks of Atlantic herring. To investigate the possible relations between chaetognaths and nontidal drift along the gulf coast, we examined the distribution and breeding of the dominant chaetognath in the samples—*Sagitta elegans*, a species predatory on larval herring (Lebour 1922, 1923). Chaetognaths have been used as indicators of water movements by many investigators (Alvarino 1965).

Information is available on the distribution and breeding of chaetognaths from several areas in the Gulf of Maine proper (Bigelow 1926; Redfield and Beale 1940; Clarke, Pierce, and Bumpus 1943), although few observations on chaetognaths have been made along the coast. Species of *Sagitta* were included in the lists of zooplankton collected in Maine waters by Fish and Johnson (1937); young S. *elegans* in Casco Bay were cited as evidence of possible summer breeding (Bigelow 1926); and seasonal catches made in the Gulf of Maine before 1934 were plotted by Redfield and Beale (1940), who showed S. *elegans* in maximal numbers in autumn along the Maine coast.

METHODS

Zooplankton was sampled along the coast from Machias Bay, Maine, to Cape Ann, Massachusetts. For comparisons of areal distributions, coastal waters were separated into three sections based on differences in hydrography (Sherman 1966)—a western area between Cape Ann and Cape Elizabeth; the central area, from Cape Elizabeth to Mt. Desert Island; and the eastern area, from Mt. Desert to Machias Bay (Fig. 1). Four stations in each of the areas were sampled in daylight hours during winter, spring, summer, and autumn in 1963–1966 (Table 1). Zooplankton was collected with a Gulf III sampler (Gehringer 1952) towed at 11 km/hr for 30 min in a step-oblique haul (10 min each at 20, 10, and 0 m). Monel netting of 0.37-mm aperture was used in the sampler. The amount of water strained for each tow was determined from a flowmeter mounted in the tail section.

Collections were also made in 1966 along three inshore–offshore transects (5 to 7 stations each) from within the headlands

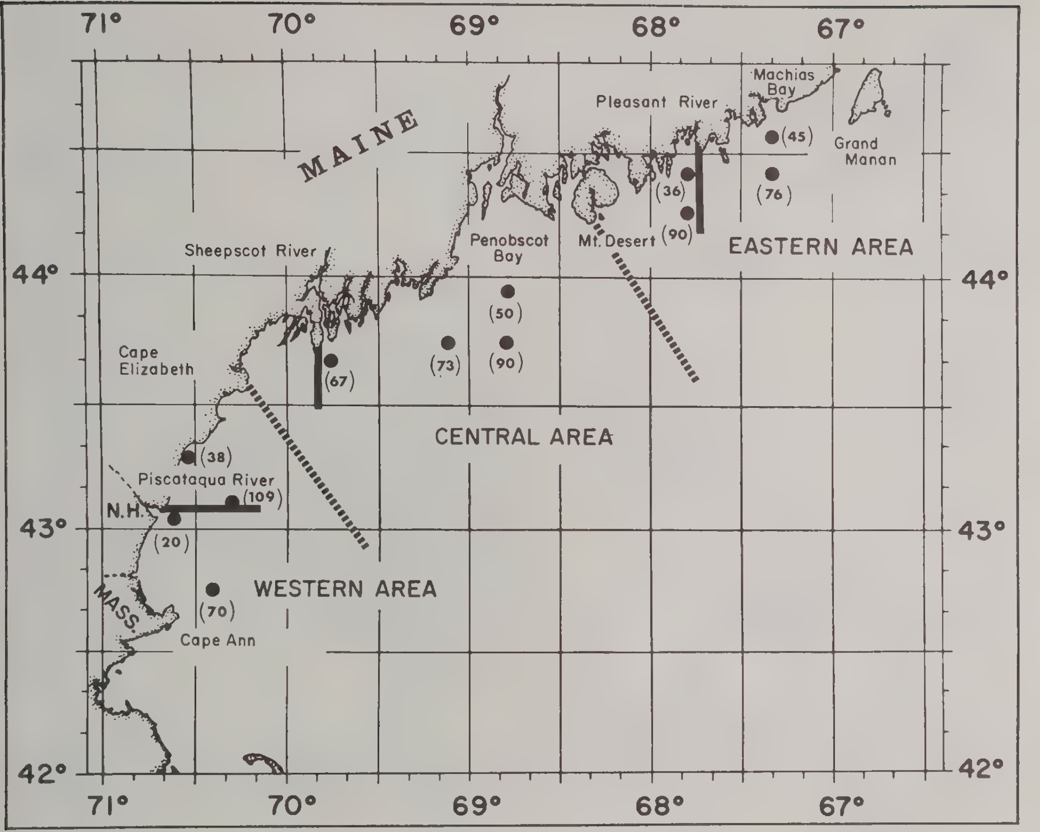
71°
70°
69°
68°
67°
MAINE
Machias Bay
Pleasant River
(45)
Grand Manan
(36)
(76)
(90)
Mt. Desert
EASTERN AREA
Penobscot Bay
Sheepscot River
44°
(50)
Cape Elizabeth
(67)
(73)
(90)
CENTRAL AREA
(38)
Piscataqua River
(109)
N.H.
43°
(20)
WESTERN AREA
MASS.
(70)
Cape Ann
42°

FIG. 1. Sampling locations for zooplankton collected in coastal waters of Maine. Broken lines separate major coastal areas; dots are station locations; solid lines show positions of inshore–offshore transects from the Piscataqua, Sheepscot, and Pleasant estuaries. Bottom depth in meters at each station is shown in parentheses.

of three estuaries—the Piscataqua, Sheepscot, and Pleasant—to approximately 28 km offshore (Fig. 1). Clarke-Bumpus samplers (Paquette and Frolander 1957) were towed during daylight hours in a vertical series at 3.7 km/hr for 15 min. Mean numbers of S. *elegans* (per 10 m^3 of water) were determined at each location for 0- and 10-m depth in the inner estuary and at 0, 10, 30, and 60 m from nearshore to offshore stations.

Chaetognaths were examined in the laboratory. All the chaetognaths in the total sample or in an aliquot (up to $\frac{1}{64}$)

TABLE 1. *Dates of coastal cruises during which* Sagitta elegans *was sampled, 1963–1966*

Season	1963	1964	1965	1966
Winter	5–16 Jan	21 Jan–14 Feb	30 Jan–7 Feb	5 Jan–6 Feb
Spring	25 May–2 Jun	21–28 May	20–26 May	17–26 May
Summer	10–22 Jul	10–20 Aug	14–28 Aug	27 Jul–7 Aug
Autumn	11–20 Oct	1–13 Oct	20–28 Oct	9–17 Oct

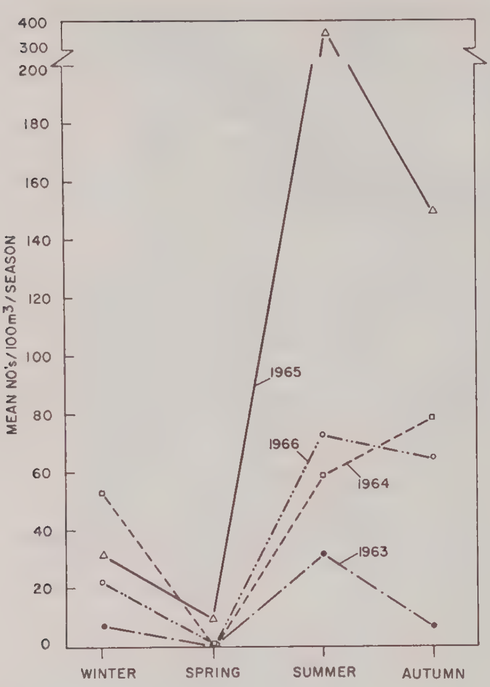

FIG. 2. Seasonal abundance of *Sagitta elegans* in coastal waters of Maine, 1963–1966, plotted as mean numbers of *S. elegans* for each season and year of sampling.

of the sample were removed. Each specimen was measured and numbers (per unit of water strained) were recorded by length and stage of maturity.

Three stages of maturity were recognized: stage 1—no ovarian development; stage 2—developing ovaries, but no visible seminal vesicles; and stage 3—well-developed ovaries and prominent seminal vesicles. A few large individuals with flaccid ovaries devoid of eggs were observed. They were similar to the spent adults described as stage 5 by Kramp (1939). Russell (1932) described the stages of maturity on the basis of ovarian and spermatocyte development. To compare our method of staging with his, we stained 100 specimens from 3 to 30 mm long with borax carmine, following the procedure of Pierce (1941). Specimens in stage 1 and 3 were similar to Russell's, but the minor development of seminal vesicles shown for his stage 2 was not evident in our specimens.

SEASONAL AND AREAL DISTRIBUTION

The abundance of *S. elegans* progressed from a spring low to a summer high and

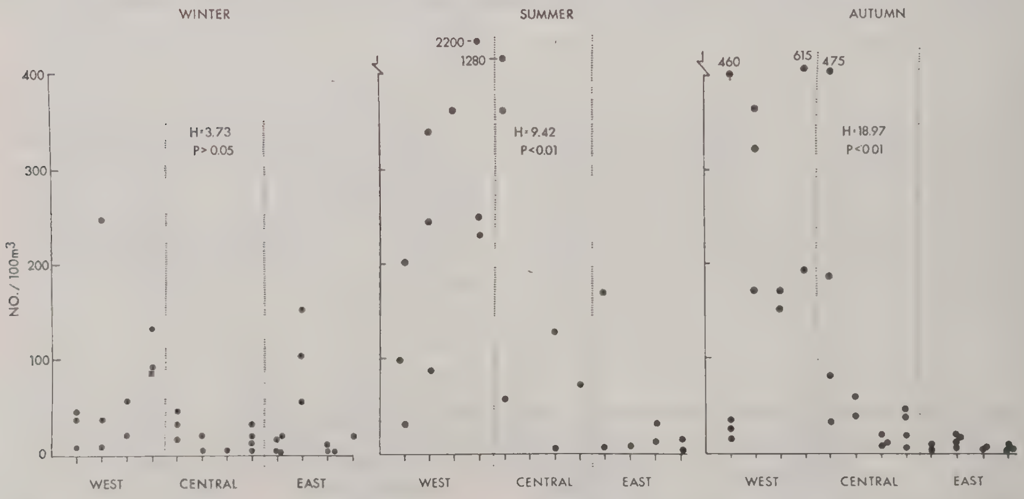

FIG. 3. Areal distribution of *Sagitta elegans* in coastal waters of Maine, 1963–1966. Kruskal-Wallis H values are given for between-area comparisons.

declined in autumn and winter, except in 1964, when the seasonal high was not reached until autumn (Fig. 2). Animals were particularly abundant during summer and autumn in 1965; volumes of zooplankton along the coast were also higher than in other years of the survey (Sherman, in press).

The distributions of *S. elegans* in the three coastal areas were tested for differences in winter, summer, and autumn using the Kruskal-Wallis one-way analysis of variance (Siegel 1956). The spring distributions were not compared because of the consistent low abundance. Differences in distribution were significant in summer and autumn ($P < 0.01$) but not in winter ($P > 0.05$). In summer, *S. elegans* was concentrated in the western and central areas; a Mann-Whitney U-test showed no differences between the eastern sector and the other areas were significant ($P < 0.05$). In autumn, concentrations in the western area were higher than in the central ($P < 0.05$) or eastern ($P < 0.001$) sectors (Fig. 3). From these data we conclude that as the year progresses the concentrations of *S. elegans* increase westward along the coast from winter, when no areal differences in abundance occurred, to autumn when maximal concentrations were in the western area.

BREEDING

The percentage occurrence of *S. elegans* was determined by maturity stages for winter, summer, and autumn 1964–1966, the seasons and years of greatest abundance in our sampling (Table 2). Stages 2 and 3 composed more than 80% of the total in winter; stage 1 made up 60 to 95% of the total in summer and autumn. Recently hatched specimens (<10 mm long) occurred most frequently in summer and autumn and larger specimens (>20 mm) in winter (Fig. 4).

Adults were examined to determine ova size in each season. Eggs of *S. elegans* when planktonic are approximately 0.33-mm diameter (Huntsman and Reid 1921) and were not retained in our nets (0.37-mm apertures). Mean diameters of ova

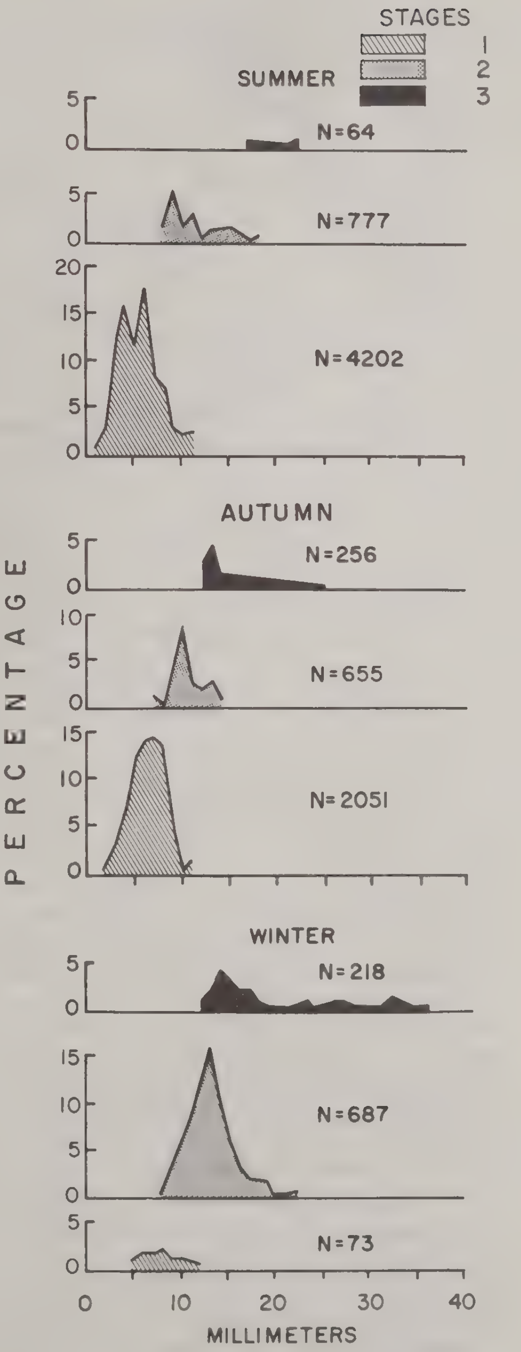

FIG. 4. Percentage occurrence of *Sagitta elegans* by length and developmental stage in summer, autumn, and winter, 1964–1966.

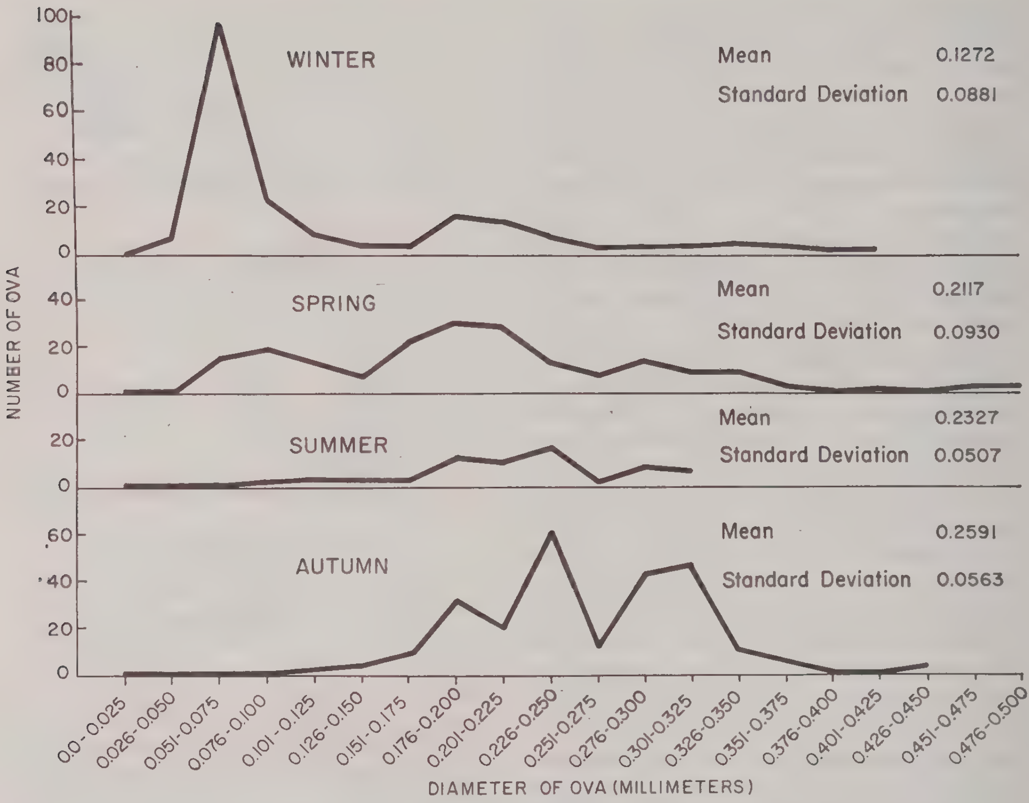

FIG. 5. Seasonal variations in the diameters of ova in the ovaries of *Sagitta elegans.*

in the ovaries were smallest in winter (<0.13 mm). Larger ova (>0.20) occurred most frequently in spring, summer, and autumn (Fig. 5). Our data indicate a prolonged period of breeding in coastal waters, beginning in late spring, and extending through autumn. The predominance of specimens with small ova and low numbers of stage 1 specimens suggests that no significant breeding occurs in winter.

ABUNDANCE AND BREEDING

The seasonal fluctuations in abundance of S. *elegans* are related to the breeding cycle and associated changes in the vertical distribution of adults. Immature S. *elegans* are in the upper waters in all seasons (Huntsman and Reid 1921; Bigelow 1926), but adult chaetognaths generally descend to the lower depths to breed and ultimately die (*see* Alvarino 1965). Although our abundance estimates of adults are minimal (because coastal sampling with the Gulf III sampler was limited to the upper 20 m), the persistent trend in the dominance of stages 2 and 3 in winter, and of stage 1 from summer through autumn, suggests that S. *elegans* breeds only once annually along the gulf coast. Apparently the low abundance in spring was caused by the combined effects of mortality and undersampling of the adults that moved to deep water (>20 m) to breed.

AREAL DISTRIBUTION AND HYDROGRAPHY

In winter, drift is poorly developed and S. *elegans* is evenly distributed along the coast. Numbers increase progressively westward in summer and autumn, apparently transported along the coast in the strong southwesterly drift (up to 9 km/

TABLE 2. *Percentage occurrence of* Sagitta elegans *by stages of maturity and season (winter, summer, autumn), 1964–1966. (Numbers of specimens are shown in parentheses)*

Year, and developmental stages	Winter	Summer	Autumn
1964			
1	2.6 (14)	74.7 (310)	70.8 (581)
2	78.2 (415)	25.3 (105)	21.9 (180)
3	19.2 (102)	—	7.3 (60)
1965			
1	6.2 (14)	81.8 (3,098)	60.5 (958)
2	50.9 (115)	16.5 (626)	27.4 (433)
3	42.9 (97)	1.7 (64)	12.1 (192)
1966			
1	20.4 (45)	94.5 (794)	91.8 (512)
2	71.0 (157)	5.5 (46)	7.5 (42)
3	8.6 (19)	—	0.7 (4)

day) developed in late summer (Bumpus and Lauzier 1965). Areal differences in abundance, therefore, appear to be influenced by nontidal drift.

Three major centers of abundance have been reported for S. *elegans* in the Gulf of Maine–Georges Bank, the Scotian Banks off Cape Sable, and Massachusetts Bay (Bigelow 1926). Because S. *elegans* is known to be widely distributed in boreal waters (Alvarino 1965), and the present study is of a limited area, it is not possible to determine quantitatively the amount of mixing, if any, that may occur among the population centers in the Gulf of Maine. It has been reported, however, that on Georges Bank the population is maintained on the bank throughout the year, with no large-scale transport shoreward (Clarke et al. 1943). On the Scotian Banks, where the waters are free of residual drifts until late summer and autumn (Redfield and Beale 1940), the population is stable until September. In September, a strong nontidal drift develops around the southern tip of Nova Scotia that apparently carries large numbers of S. *elegans* into the Bay of Fundy during autumn and winter (Huntsman and Reid 1921). Transport to the northeast corner of Maine may also occur, but the consistently low numbers of all stages of S. *elegans* in the eastern area in autumn indicate a lack of significant augmentation from the Scotian Banks region. In addition, no concentrations of S. *elegans* have been reported from the deep basin

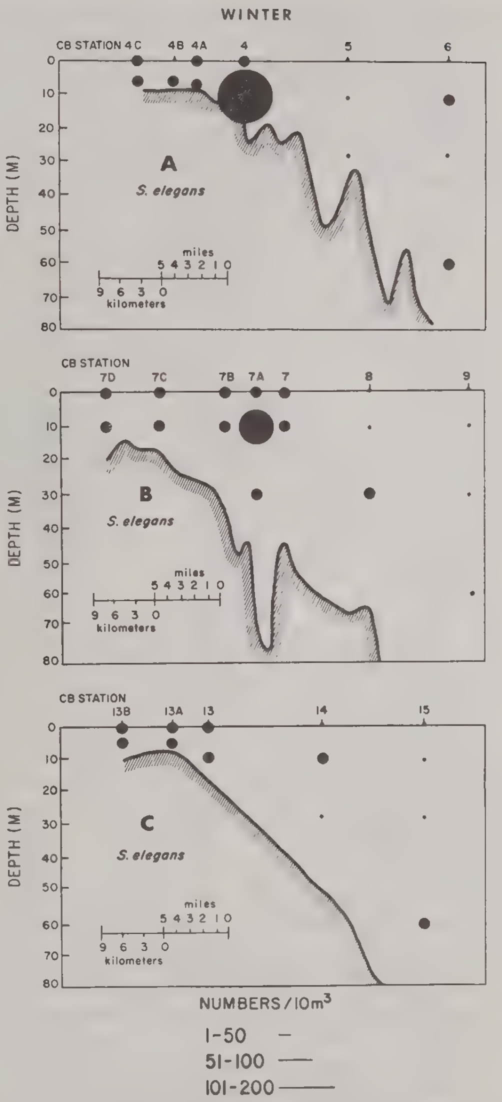

FIG. 6. Inshore–offshore and vertical distribution of S. *elegans* in three Gulf of Maine estuaries (A) Piscataqua, (B) Sheepscot, and (C) Pleasant, in winter 1966. Dots represent positions of the tows; width of the other symbols represent the numbers of S. *elegans* per 10 m³ of water strained.

TABLE 3. *Seasonal occurrence of* Sagitta elegans *in estuarine to offshore transects, Maine coastal waters, 1966*

Estuary, and stations inshore to offshore	Location		Mean number of *S. elegans*/10 m³/station			
	N lat	W long	Winter	Spring	Summer	Autumn
Piscataqua						
4C	43°06′	70°47.5′	13	2	—	11
4B	43°05′	70°44.5′	6	—	5	15
4A	43°04′	70°42.5′	22	4	13	4
4	43°02′	70°39′	83	—	20	35
5	43°02′	70°29′	—	—	2	—
6	43°02′	70°19′	1	1	—	—
Sheepscot						
7D	43°57.5′	69°40′	36	—	2	2
7C	43°54′	69°41.5′	18	1	—	1
7B	43°49′	69°42.5′	25	—	—	10
7A	43°47′	69°42′	34	—	36	40
7	43°47′	69°41.5′	6	—	—	73
8	43°38′	69°41′	1	—	12	3
9	43°31′	69°40′	—	—	—	6
Pleasant						
13B	44°32.5′	67°46.5′	17	—	—	2
13A	44°29′	67°47′	16	—	—	1
13	44°26′	67°47′	4	—	4	—
14	44°20′	67°45′	1	—	—	1
15	44°12′	67°43′	1	2	1	1

or the eastern channel of the gulf (Bigelow 1926; Redfield and Beale 1940). From these observations it appears that there is little movement of S. *elegans* from other population centers in the Gulf of Maine to the coast north of Massachusetts Bay. The high concentrations of stage 1 specimens in summer and autumn in the coastal areas sampled are apparently the result of local breeding and not immigration from other population centers in the gulf.

To maintain an endemic population in coastal waters, some S. *elegans* must remain within the coastal zone out of the influence of the dominant southwesterly drift. Huntsman and Reid (1921) have noted that S. *elegans* is transported into estuaries in the Bay of Fundy in the relatively high-salinity, dense bottom layer, and transported seaward in the lighter, less saline surface waters. To investigate the possibilities of inshore transport, we examined the distribution of S. *elegans* in 1966 in three estuaries—the Piscataqua, Sheepscot, and Pleasant. No concentrations of S. *elegans* were found in the seaward ends of the transects during any of the seasons at any of the depths sampled. The inshore–offshore and vertical extent of sampling is represented by the winter distribution of S. *elegans* shown in Fig. 6. S. *elegans* was in the estuaries during winter, summer, and autumn but rarely occurred in spring (Table 3). We do not know what specific mechanisms affect the retention of S. *elegans* in the coastal-estuarine environment. Older specimens, however, known to favor the lower depths, may be retained in the estuaries for longer periods than younger forms more commonly found in the upper waters; a continuous exchange between S. *elegans* on the coast and in the estuaries could be maintained by water movements generated by tidal flow or two-layered transport.

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PONTELLID COPEPODS AS INDICATORS OF AN OCEANIC INCURSION OVER GEORGES BANK

By

KENNETH SHERMAN AND EVERETT SCHANER

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PONTELLID COPEPODS AS INDICATORS OF AN OCEANIC INCURSION OVER GEORGES BANK

KENNETH SHERMAN AND EVERETT SCHANER
Bureau of Commercial Fisheries Biological Laboratory, W. Boothbay Harbor, Maine 04575

(Accepted for publication March 15, 1968)

Abstract. The distribution of pontellid copepods was used to delineate the region of mixing between coastal and oceanic surface waters during an incursion of Gulf Stream water over Georges Bank. The greatest changes in the distribution of pontellids were at 21°C and between 32.5 ‰ and 33.0 ‰ salinity.

An incursion of warm surface water of probable Gulf-Stream origin was observed over the southern part of Georges Bank in the summer of 1966, during a cruise of the Bureau of Commercial Fisheries vessel *Albatross IV*. Similar occurrences have previously been reported (Bigelow 1926; Colton 1959; and Colton, Temple, and Honey 1962). To supplement physical oceanographic data on the movements of the warm waters, and to delineate the region of faunal change between coastal and oceanic waters, we examined the distribution of pontellid copepods collected during the cruise. Previous studies have shown that pontellids are abundant in the surface waters, and that several species are limited to discrete types of water (Heinrich 1960, 1964; Voronina 1962, 1964; Sherman 1963, 1964).

METHODS

Pontellids were collected in 51 surface plankton tows in the Gulf of Maine and at Georges Bank (Fig.1). Tows were made with a 2- by 1-m rectangular frame and attached net of 1.0 mm nitex apertures. The net was hauled at 6 knots for 30 min at each sampling location, and strained approximately 5,600 m^3 of water per tow; only the lower half of the net was in the water during the tow. The sampling was designed to catch larval lobsters; catches of pontellids were incidental. Pontellids were separated from the total sample or an aliquot (as small as 1/64), and enumerated by species.

SPECIES COMPOSITION AND RELATIVE ABUNDANCE

The samples contained 11 species of pontellids. The predominant pontellid was *Anomalocera patersoni* (ca.

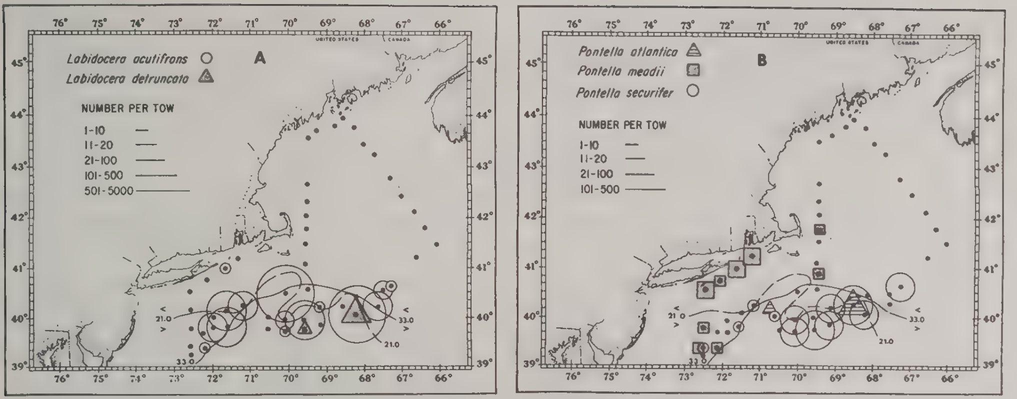
A
Labidocera acutifrons ○
Labidocera detruncata △
NUMBER PER TOW
1-10
11-20
21-100
101-500
501-5000
B
Pontella atlantica △
Pontella meadii ▨
Pontella securifer ○
NUMBER PER TOW
1-10
11-20
21-100
101-500
21.0
33.0
UNITED STATES
CANADA

FIG. 1. Horizontal distribution of *Labidocera acutifrons* and *L. detruncata* (A) and *Pontella securifer, P. atlantica,* and *P. meadii* (B) in relation to surface salinity and temperature. *Albatross* IV Cruise 66–10, July–August 1966. Dots show station locations; width of symbols indicate ranges of pontellid abundance in numbers per tow. Solid line is the 33 ‰ isohaline; broken line is 21°C isotherm.

3,000/tow) followed by *L. acutifrons* (ca. 50/tow), *P. regalis* (ca. 20/tow), and *P. securifer* (ca. 10/tow). [The *P. securifer* females were similar in abdominal structure to the description given by Giesbrecht (1892) for *P. spinipes*. We, however, have followed Fleminger (1965), and consider our specimens to be low dimorphs of *P. securifer*.] The remaining species were less numerous (< 2/tow): *Pontella meadii* Wheeler, *P. atlantica* (Milne Edwards), *P. mimocerami* Fleminger, *Labidocera aestiva* Wheeler, *Pontellopsis villosa* Brady, *Labidocera detruncata* (Dana), and *Anomalocera ornata* Sutcliffe.

HORIZONTAL DISTRIBUTION OF PONTELLIDS AND SURFACE WATER TYPES

The temperatures in the sampling region varied 14.5°C, from 8.9°C in the South Channel to 23.4°C on the southern margin of Georges Bank. Salinity ranged from 31.46 ‰ off the coast of southern Maine to 35.30 ‰ on the southern edge of Georges Bank.

Temperature-salinity-pontellid (T-S-P) distributions were constructed (Sherman 1963) for each species to determine the relations between pontellids and hydrographic conditions. The greatest changes in the concentrations of pontellids occurred at approximately 21°C and between 32.5 ‰ and 33.0 ‰.

Three types of water have been described for the region off the New England coast: coastal water of < 35.0 ‰ salinity, Gulf Stream water with salinities > 36.0 ‰, and Slope water, representing a zone of mixing between coastal water moving seaward and Gulf Stream water moving north of the main axis of drift (Iselin 1936; McLellan 1957). In the region of sampling, during August 1966, the northern edge of the Gulf Stream, as located by airborne infrared radiation surveys was at approximately 40°31′N and 65°31′ to 69°00′W (Anonymous 1966). A marked break in the distribution of pontellid copepods was also close to this position, and within 80 km of the 33.0 ‰ isohaline and 21.0°C isotherm. Five species were most numerous on the oceanic side of the isolines—*Labidocera acutifrons, L. detruncata, Pontella atlantica, P. securifer* (Fig. 1) and *Pontellopsis regalis* (Fig. 2). These species have previously been associated with high salinity and warm oceanic waters (Heinrich 1960, 1964; Voronina 1962, 1964; and Sherman 1963,

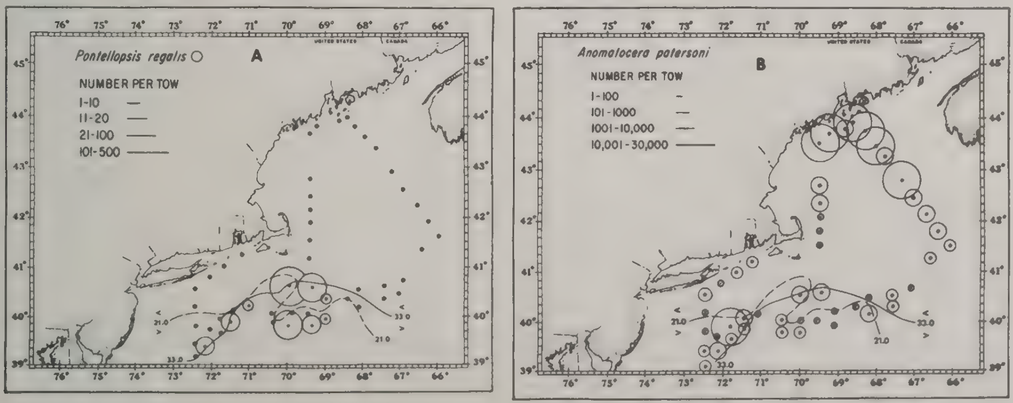
A
Pontellopsis regalis ○
NUMBER PER TOW
1-10
11-20
21-100
101-500
B
Anomalocera patersoni
NUMBER PER TOW
1-100
101-1000
1001-10,000
10,001-30,000
21.0
33.0
UNITED STATES
CANADA

FIG. 2. Distribution of *Pontellopsis regalis* (A) and numbers of *Anomalocera patersoni* per tow (B) in relation to surface salinity and temperature. *Albatross IV* Cruise 66–10, July–August 1966. Dots show station locations; width of symbols indicate ranges of pontellid abundance in numbers per tow. Solid line is the 33 ‰ isohaline; broken line is the 21°C isotherm.

1964). In contrast, the greatest concentrations of *Anomalocera patersoni* (Fig. 2) and *Pontella meadii* (Fig. 1) were on the coastal side of the boundary region in the cooler, less saline water. These findings are consistent with previous reports of *P. meadii* from neritic waters in the Gulf of Mexico (Fleminger 1957) and *A. patersoni* from water "intermediate" to neritic and oceanic conditions (Bigelow 1926; Glover 1961). The remaining species—*Anomalocera ornata, Labidocera aestiva, Pontella mimocerami,* and *Pontellopsis villosa*—occurred in low numbers at only one or two locations; conclusions regarding their distributions among water types cannot be made.

Oceanic fronts have been described as boundary regions between unlike surface water types (Clarke and Laevastu 1967). Although the specific limiting factors have not been determined, the discontinuity in pontellid distribution at the northern edge of the Gulf Stream probably represents a faunal boundary region between coastal and oceanic waters. Similar discontinuities in distributions of pontellids have been found between different surface water types in other areas (Heinrich 1960, 1964; Voronina 1962, 1964; Sherman 1963, 1964). It is likely that the oceanic group of pontellids was carried over the southern margin of Georges Bank in the northward extension of the main axis of the Gulf Stream. This movement was first observed in July 1966 between 65° and 69°W, off the New England coast (Anonymous 1966). The occurrence of moderate numbers of *A. patersoni* (ca. 400/tow) on the oceanic side of the boundary suggests that the Gulf Stream water was advected over an area on Georges Bank that was previously populated by a boreal-neritic fauna.

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MOVEMENT AND RECOVERY OF TAGGED KING CRABS IN THE EASTERN BERING SEA, 1955–63

by
Robert R. Simpson and Herbert H. Shippen
Biological Laboratory, Bureau of Commercial Fisheries
Seattle, Washington

ABSTRACT

More than 32,000 adult male king crabs, *Paralithodes camtschatica* (Tilesius), were tagged and released in the eastern Bering Sea in 1955–61. Carapace lengths ranged from 4 to 20 cm. Tagged crabs were recaptured in commercial king crab fisheries of Japan, the U.S.S.R., and the United States; by the end of the 1963 fishing season 14 percent of the tagged crabs had been returned.

Tagging and recovery data suggest that king crabs of the eastern Bering Sea constitute a single population, in which individuals move and mix randomly. Growth in length of male crabs averaged about 1 cm per year. Half of the tags returned were from crabs caught within 50 nautical miles of the locality of release. The longest distance traveled by a crab in a single year was 230 nautical miles.

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Bull. 24, Int. North Pac. Fish. Comm., 1968.

INTRODUCTION

As part of the United States research program under the International North Pacific Fisheries Commission (INPFC), the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington, attempted to determine the factors which affect the yield of the king crab, *Paralithodes camtschatica* (Tilesius), in the eastern Bering Sea. To study growth and mortality, large numbers of king crabs were tagged and released during the summer months of 1955–61. Tag returns considered here were made by fishermen of the United States, Japan, and the Soviet Union in 1955–63.

Tag return rates, distances traveled by marked king crabs, relative abundance of crabs within regions of the eastern Bering Sea, sizes of crabs taken by the commercial fishery, and size at recruitment are discussed. Background information is offered on the historical development of the fishery, and the main fishing areas and geographic limits of the resource in the eastern Bering Sea are described.

Field work was done in an area of about 40,000 nautical square miles of the eastern Bering Sea north and east of Unimak Island (Figure 1). Water depth in the area is less than 50 fathoms; most of the commercial crab fishing is in 30–40 fathoms.

King crabs were tagged from May through August; recoveries were made during commercial fishing for this species from spring through early fall. Winter operations, both commercial crab fishing and tagging, were prohibited by inclement weather.

KING CRAB FISHERIES OF THE EASTERN BERING SEA

Fishermen of Japan, the Soviet Union, and the United States fish for king crabs in the eastern Bering Sea (Figure 2). The method of fishing used by the Japanese and Soviet fishermen has traditionally been the tangle net, a type of stationary bottom net that entangles crabs as they attempt to pass through the meshes (Miyahara, 1954). United States fishermen used otter trawls from 1947–60, but since 1963 fishing

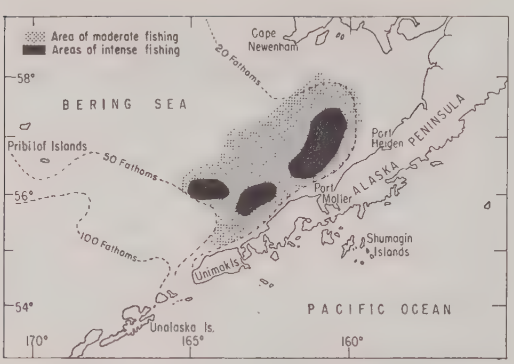

FIGURE 1. Eastern Bering Sea, showing king crab fishing areas.

has been conducted with crab pots, as in the Kodiak Island area (Allen, 1964). Agreements by the United States with Japan (1964) and the Soviet Union (1965) have designated an area north of Unimak Island in which only pot fishing is to be permitted.

THE JAPANESE FISHERY

Japanese king crab fishing in the eastern Bering Sea began in 1930 when a factoryship fleet caught and processed about one million king crabs. In 1932–39 the total catch was 6.8 million king crabs which yielded 170,000 cases (48 one-pound cans per case). Fishing by Japan was discontinued from 1940 through 1952, but was resumed in 1953 under regulation by the Fisheries Agency of Japan. (Miyahara, 1954.)

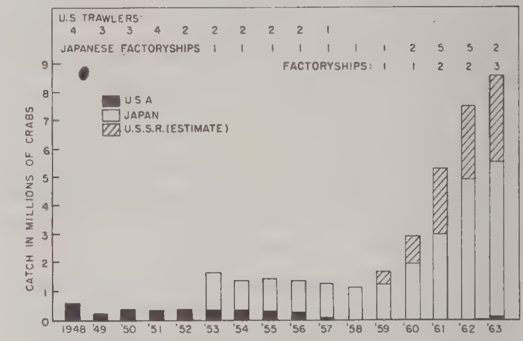

FIGURE 2. King crab fishery in the eastern Bering Sea, 1948–63. Sources: INPFC Statistical Yearbooks 1952–1963, except as follows: United States in 1948–52—unpublished data at the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington; United States in 1963—State of Alaska catch records; Soviet catch data is estimated.

From 1.06 to 1.29 million crabs were taken annually in 1953–59 by a single factoryship. Beginning in 1960, Japan increased the production quota and dispatched additional factoryships to the area. In 1961 a fall fishing season was instituted. As a result of this accelerated effort, catches by Japan increased to 5.5 million king crabs in 1963. The growth of the Japanese king crab operations in the eastern Bering Sea in 1959–63 is summarized in Table 1.

TABLE 1. Japanese king crab operations in the eastern Bering Sea, 1959–63.

Year and season	Factoryships*	Catch[1] (millions of crabs)
1959, spring and summer	*Tokei Maru* (C)	1.3
1960, spring and summer	*Tokei Maru* (C) *Shinyo Maru* (F)	1.9
1961, spring and summer	*Tokei Maru* (C) *Shinyo Maru* (F)	1.9
1961, fall	*Banshu Maru No. 31* (F) *Eishin Maru* (F) *Chichibu Maru No. 2* (F)	1.1
1962, spring and summer	*Tokei Maru* (C) *Shinyo Maru* (F) *Dainichi Maru* (C)	3.2
1962, fall	*Shinyo Maru* (F) *Ishiyama Maru* (F)	1.7
1963, spring, summer, and fall	*Tokei Maru* (C) *Dainichi Maru* (C)	5.5

* C=Cannery; F=Freezer

[1] Catch data from INPFC Statistical Yearbooks for 1959 through 1963; vessel names obtained from data sheets accompanying tag returns.

THE UNITED STATES FISHERY

Commercial king crab fishing by the United States in the eastern Bering Sea began in 1947 when three otter trawlers caught and processed an estimated 120,000 crabs into 170,000 pounds of frozen meat (Pacific Fisherman, 1948). In 1952–56 the annual catch averaged about 330,000 crabs. A single U.S. trawler caught 107,000 crabs in 1957. Only 900 crabs were taken in a few days of trawling in 1958, and 36,000 were caught in 1960. United States king crab vessels did not operate in the Bering Sea in 1959 or 1961. (From INPFC Statistical Yearbooks.)

THE SOVIET UNION FISHERY

King crab fishing by the U.S.S.R. started in the eastern Bering Sea in 1959 when a factoryship entered the area in an exploratory operation. The vessel returned to the eastern Bering Sea in 1960 as a regular fishing assignment, and was joined by a second factoryship in 1961. In 1963 the Soviet fleet consisted of

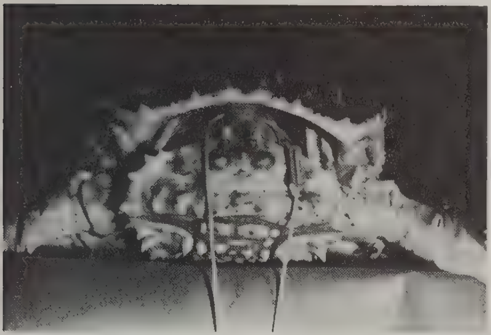

FIGURE 3. Posterior view of king crab with spaghetti tag through arthral muscle.

three large new vessels. No official catch statistics are available for fishing by the U.S.S.R.

TAGGING OPERATIONS

The United States tagged king crabs in the eastern Bering Sea each year from 1954 to 1961. In 1954, crabs caught by a U.S. commercial trawler were marked with Petersen disk tags attached to the carapace or to a leg by a nickel pin. The usefulness of tags attached to the external skeleton is negligible in studies which require individuals to remain marked, because tags are lost during molting. In 1955–61, a tubular plastic or "spaghetti" tag was used. This type of tag and its point of attachment had been used previously by the Alaska Department of Fisheries (Alaska Fisheries Board and Alaska Department of Fisheries, 1955), and modifications have been documented by Gray (1965). The spaghetti tag was attached to the flesh rather than to the exoskeleton and remained with the crab throughout successive molts. Information used in this report is limited to that based on experiments in which spaghetti tags were used.

METHODS AND MATERIALS

The spaghetti tags consisted of yellow, white, or red plastic tubing (about 18″ long, 1/12″ outside diameter) strung through two holes in a colored laminated plastic button (1″ long, ¼″ wide, 1/32″ thick) that bore an identifying legend. A curved needle, fabricated from 1/16″ diameter stainless steel rod and about 5″ long, was used to attach the tag. One end of the needle was pointed and the other was reduced to fit tightly into one end of the plastic tubing. The point of attachment to the crab was the arthral muscle at the junction of the cephalo-thorax and the abdomen, an area sometimes termed the isthmus. The arthral muscle was exposed by raising the posterior margin of the carapace, and the plastic tubing was passed through it (Figure 3). The needle was detached, and the loose ends were tied with an overhand knot. The tag thus formed a small loop around the arthral muscle.

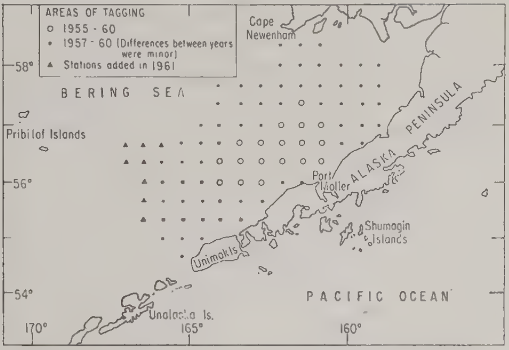

FIGURE 4. Stations at which king crabs were tagged in 1955–61.

AREA OF TAGGING

King crabs for tagging were captured by an otter trawl fished from a chartered vessel. The trawl was of the 400-mesh "eastern type" (Greenwood, 1958). The tagging period extended from April to August. Stations were on a rectangular grid at 20-mile intervals (Figure 4). In addition to the tagging at stations in the grid, large numbers of crabs were tagged in 1957–59 at other locations where scouting by means of short tows had indicated concentrations of adult males.

In 1955 and 1956, tagging was done only in the general area of the commercial fishery (see Figure 1). Beginning in 1957 the distribution of stations was expanded to include most of the eastern Bering Sea in which adult male crabs were common. This expansion was accomplished by continuing the establishment of stations at intervals of 20 miles at the outer end of each grid line until the number of male crabs per standard trawl effort fell to less than 10. In 1955–57 the standard trawl effort was a ½-hour tow; in 1958–61 it was a 1-hour tow. Standard hauls were made at each station of the original grid four times in 1955 and twice in 1956, and at stations of the expanded grid once in 1957 and 1960 and twice in 1958. In 1959 and 1961, inclement weather and other factors prevented sampling at some stations of the expanded grid.

COLLECTION OF INFORMATION AT TIME OF RELEASE

At each tagging station the king crabs were counted and sexed, shell conditions were noted, and carapace lengths (the distance between the right orbital socket to the median indentation of the posterior margin of the carapace) were measured. Because commercial king crab fisheries retain only the larger males for

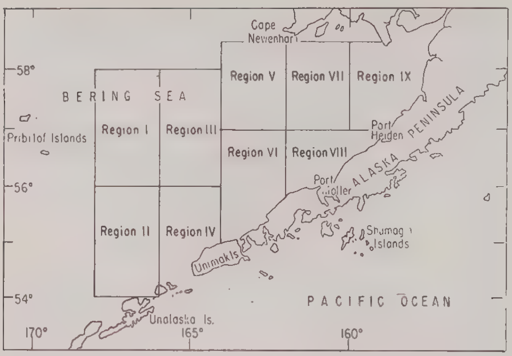

FIGURE 5. Regional division of the eastern Bering Sea used in this report.

processing, only viable males were tagged. All crabs were released either on station or as the vessel proceeded toward the next station.

Shell condition was classified as either soft, new, old, or very old. Criteria for these categories were the varying degrees of shell hardness, discoloration, scratch marks, and growth of fouling organisms. Generally, "soft" shells were pliable and clean; "new" shells were firm, clean, and without scratch marks; "old" shells were firm, discolored, scratched, and with or without fouling organisms; and "very old" shells were firm and very discolored, with many scratch marks, and usually with much growth of fouling organisms.

DATA PROCESSING

Automatic data processing cards were used to store most of the data relevant to each tag returned, including tag number, sex, date, location, size, and shell condition at release and recovery. Locations of release and recovery of tagged king crabs were entered on the cards in terms of latitude and longitude. A conversion deck was used to change the latitude and longitude designation to a hierarchical-plot system consisting of nine regions (Figure 5) and eight areas within each region. Boundaries between regions were drawn arbitrarily along geographic lines and had no known biological basis.

RELEASES OF TAGGED MALE CRABS

In 1955–61, 32,214 male king crabs were marked with spaghetti tags and released in the eastern Bering Sea; of this total, 14,981 were released at stations in the rectangular grid, and 17,233 were released in areas of concentration located by scouting. Crabs released at the established stations were used to provide estimates of relative abundance in the nine regions of release. All crabs tagged in a particular region were used to study movement into the area of the commercial fishery.

In 1955–56 only male crabs with carapaces about 12 cm or longer were tagged. Beginning in 1957, however, all males large enough to accommodate a tag (carapace length 7 cm or more) were marked (Table 2).

The mean carapace length of all male king crabs

TABLE 2. Frequency distribution of carapace lengths of tagged male king crabs at time of release.

Length (cm)	No. of crabs by year of release							Total
	1955	1956	1957	1958	1959	1960	1961	
4	—	—	—	1	—	—	—	1
5	—	—	2	1	—	—	—	3
6	—	—	7	8	—	—	—	15
7	—	—	97	58	1	1	—	157
8	—	—	139	274	3	10	19	445
9	—	1	319	573	55	37	95	1,080
10	3	16	1,264	348	187	91	74	1,983
11	56	70	2,782	401	259	142	97	3,807
12	136	285	2,732	722	258	179	209	4,521
13	216	496	2,099	853	520	188	231	4,603
14	277	625	1,653	698	1,014	225	342	4,834
15	214	765	1,350	648	1,027	192	489	4,685
16	197	519	873	466	745	162	662	3,724
17	173	191	369	292	300	89	422	1,836
18	67	38	83	64	65	12	131	460
19	12	6	12	3	8	1	15	57
20	—	1	—	1	—	—	1	3
Total	1,351	3,013	13,781	5,511	4,442	1,329	2,787	32,214

Table 3. Frequency distribution of carapace lengths of tagged male king crabs, by region of release.

Length (cm)	No. of crabs by region of release[1]									Total
	I	II	III	IV	V	VI	VII	VIII	IX	
4	—	—	—	—	—	—	1	—	—	1
5	—	—	—	—	—	—	2	—	2	4
6	—	—	—	—	—	—	8	5	2	15
7	—	—	—	1	2	27	66	50	11	157
8	—	—	2	25	28	79	188	115	8	445
9	—	—	74	90	117	292	308	189	10	1,080
10	—	—	614	277	97	673	186	128	8	1,983
11	—	—	1,900	410	100	1,082	196	110	9	3,807
12	—	—	2,324	483	240	1,106	205	153	10	4,521
13	8	1	2,130	554	475	1,038	217	173	7	4,603
14	38	5	1,953	559	773	975	278	243	10	4,834
15	73	3	1,755	468	860	916	317	279	14	4,685
16	127	4	1,393	335	523	723	336	281	2	3,724
17	82	4	700	173	165	365	170	174	3	1,836
18	9	2	180	48	32	103	31	55	—	460
19	1	—	19	10	4	15	5	3	—	57
20	1	—	—	—	—	1	1	—	—	3
Total	339	19	13,044	3,433	3,416	7,395	2,514	1,958	96	32,214

[1] See Figure 5.

tagged was 13.3 cm (range, 4 to 20 cm). Most of the smaller crabs tagged were from the eastern part of the area (Table 3). More than 22 percent of the male crabs tagged in Region VII and 18 percent in Region VIII were less than 10 cm in carapace length.

RECOVERY PROCEDURES

In 1955–63, 4,585 tagged male king crabs, 14.2 percent of the number tagged, were returned from the eastern Bering Sea. An additional 72 tags were returned without exact information on location of recovery; these crabs have not been considered. Some of the tagged crabs had been at liberty for seven years before recapture.

Principal Fishing Grounds

Areas from which the largest numbers of tagged crabs were returned coincided with areas of greatest fishing effort (Table 4, Figure 6). Commercial fishing was concentrated in a zone that included most of Regions VI and VIII. In this inshore zone, king crabs congregate to mate during the spring. It is only since 1961 and the start of the offshore fishery during the fall that the southern part of Region III has become part of the zone of intensive fishing.

More than 90 percent of the recoveries of tagged crabs were made within the principal fishing zone. Statistics are available by area on United States and Japanese commercial catches for 1955–60; in each of

Table 4. Number of king crabs caught in the eastern Bering Sea by Japanese and United States fishermen, 1955–60.

Region[1]	No. of crabs by year[2]						Total	Percentage of total
	1955	1956	1957	1958	1959	1960		
III	56,983	34,754	40,809	—	—	—	132,546	1.6
IV	—	2,472	—	—	—	2,205	4,677	0.1
V	102,895	131,879	61	—	—	—	234,835	2.9
VI	155,925	313,512	581,952	291,256	1,177,049	836,322	3,656,016	45.0
VII	328,493	292,179	—	51,370	—	—	673,042	8.3
VIII	793,404	597,489	655,618	487,027	144,567	779,907	3,428,014	42.2
Total	1,437,700	1,373,285	1,278,440	1,129,653	1,291,618	1,618,434	8,129,130	100.1

Source: Individual fishing company records.

[1] See Figure 5.

[2] Detailed data on catch by region are not available after 1960.

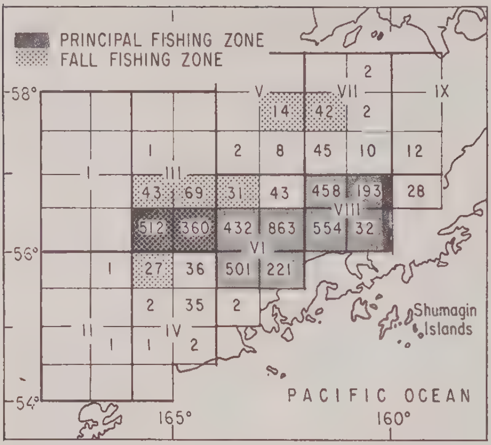

Figure 6. Return of 4,585 tagged male king crabs, by area, 1955–63.

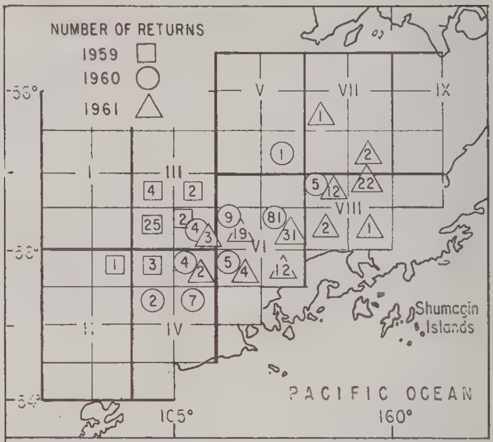

Figure 7. Tag returns from the U.S.S.R. king crab fishery, 1959–61.

these years except 1956, the principal fishing zone accounted for nearly all of the commercial crab catch.

Official statistics on U.S.S.R. catches are not available. However, 266 tags were returned from that country's Bering Sea fishery in 1959–61. These returns indicate that the 1959 Soviet fishery was in the offshore westward portion of the eastern Bering Sea, but that during 1960–61 operations were nearer the Alaska Peninsula, in the zone traditionally fished by the Japanese (Figure 7). The Soviet tag returns accounted for nearly 15 percent of the total tags returned in the period 1959–61.

Adequacy of Tag-Recovery Data

Favorable aspects:

1. Co-operation by the Japanese was excellent. Most of the recovered crabs were measured, and relevant information was supplied by fishery biologists aboard the factoryships.

2. The detection of recovered tagged crabs was considered to be good because each crab was handled individually before processing. No estimate was obtained, however, of the percentage of tagged crabs recovered but not returned.

Unfavorable aspects:

1. Fishing was usually confined to a few inshore areas and to only a few months. Fishing over a greater area and for a longer season would have provided better information on movements of king crabs.

2. Recording of the recovery position for tagged crabs was only approximate. The Japanese used the position of the factoryship at noon each day as the location of tag recovery, although the catcher boat actually may have captured the tagged crab at some distance from the factoryship.

3. The following information was not available during the preparation of this report: (a) U.S.S.R. catch statistics; (b) U.S.S.R. tag recoveries after 1961; and (c) tag returns from the Japanese vessel *Shinyo Maru*, which took 422,000 crabs during the spring of 1961.

RATE OF RETURN OF KING CRABS

With the exceptions noted above, it seems reasonable to assume that the tagged king crabs returned by the commercial fisheries represent nearly all that were recovered; for purposes of analysis, the rate of return is considered to be essentially the same as the rate of recovery. A manuscript using tag return data to develop estimates of natural mortality rates for king crab is in preparation by Mr. George Hirschhorn of the Seattle Biological Laboratory.

Rate of Return by Year of Release

The rate of return for crabs released in each year from 1955 through 1961 and returned during 1955–63 ranged from 11.6 to 22.0 (Table 5). The 22-percent return from 1961 releases is an underestimate of the recovery because it does not include any recoveries made by the U.S.S.R. in 1962–63. In contrast to this high rate of return, at least four years of fishing were required for a return of 10 percent from crabs released before 1960. The rapid rate of recovery of crabs tagged in 1961 probably resulted from the increased fishing effort during 1962 and 1963.

Rate of Return by Region of Release

By region of release, the percentage of tagged crabs returned ranged from 22.7 in Region I to 12.6 in Region IV (Figure 8). Most of the returns from Region I were from crabs tagged in 1961; the high rate of recovery from that region was consistent with the high rate of return from all crabs tagged in 1961. The percentage of tagged crabs returned from the southern half of Region IV (near Unimak Island) was 4.3—smaller than that for any similar zone within the nine regions. This low rate suggests that some of the crabs in the southern part of Region IV may not enter the principal fishing area of the eastern Bering Sea.

DISTRIBUTION AND RELATIVE ABUNDANCE

None of the king crabs tagged in the eastern Bering Sea was reported as recaptured on the Pacific Ocean side of the Alaska Peninsula or the Aleutian Islands. In a 1957 study to determine whether crabs released in the Pacific Ocean might enter the Bering Sea, about 2,000 male king crabs were tagged in the vicinity of the Shumagin Islands and False Pass; more than 275 tags were returned by August 15, 1962, but none was from the Bering Sea (Hayes and Montgomery, 1962). Apparently adult male king crabs of the eastern Bering Sea and of the northern Pacific Ocean represent separate stocks.

TABLE 5. Summary of adult male king crabs tagged in the eastern Bering Sea from 1955 to 1961, and returned in 1955–63.

Year	Releases (no. of crabs)	Returns 1955–63 (no. of crabs)	Return rate (percent)
1955	1,351	166	12.3
1956	3,014	515	17.1
1957	13,775	1,599	11.6
1958	5,516	914	16.6
1959	4,442	594	13.4
1960	1,329	185	13.9
1961	2,787	612	22.0
Total	32,214	4,585*	14.2

* Not including 72 tag returns for which recovery location information was not supplied.

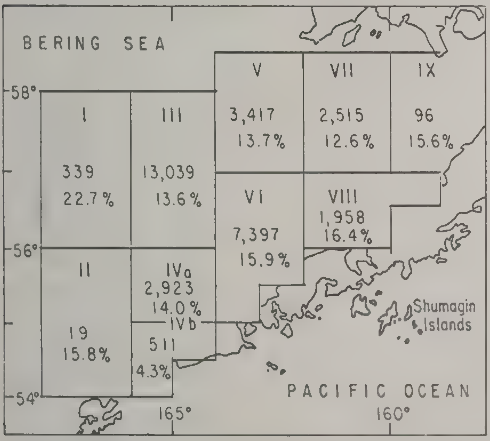
BERING SEA
58°
56°
54°
I
339
22.7%
II
19
15.8%
III
13,039
13.6%
IVa
2,923
14.0%
IVb
511
4.3%
V
3,417
13.7%
VI
7,397
15.9%
VII
2,515
12.6%
VIII
1,958
16.4%
IX
96
15.6%
Shumagin Islands
PACIFIC OCEAN
165°
160°

FIGURE 8. Number of male king crabs tagged (1955–61) and percentage returned (1955–63), by region of release. Region IV is divided to show the low rate of recovery of crabs tagged in the inshore portion.

GEOGRAPHIC LIMITS OF THE RESOURCE IN THE EASTERN BERING SEA

Early life history stages of the king crab of the eastern Bering Sea appear to be restricted to inshore waters along the Alaska Peninsula. Japanese biologists aboard the factoryships reported that most of the juvenile crabs they found were attached to seaweed fouled in tangle nets. Large numbers of immature crabs, found in shallow water in Region VIII, were smaller than 2.0 cm in carapace length (INPFC Annual Report for 1957).

Data from sampling and tagging were used to delineate the approximate geographic bounds of the king crab resource of the eastern Bering Sea. Because tagging stations were added to the periphery of the grid until catches decreased to fewer than 10 male crabs per standard trawl effort, the outer stations marked the approximate limits of distribution of significant numbers of male king crabs (Figure 9). Accordingly, the western limit of the eastern Bering Sea king crab resource was considered to be at 168°W longitude and the northern limit near 58°30′N latitude.

RELATIVE ABUNDANCE OF MALE KING CRABS BY REGION

Estimates of the relative abundance of male king

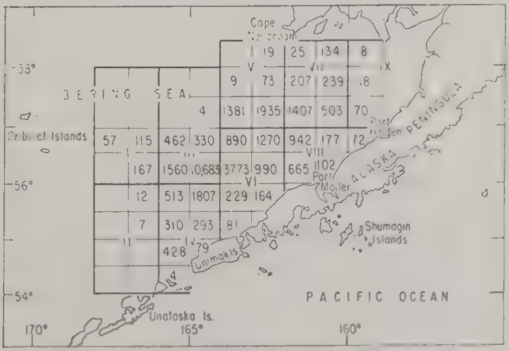
Cape
BERING SEA
Pribilof Islands
58°
56°
54°
I
II
III
IV
V
VI
VII
VIII
IX
19
25
134
8
9
73
207
239
8
4
1381
1935
1407
503
70
57
115
462
330
890
1270
942
177
72
167
1560
10,683
3773
990
665
1102
12
513
1807
229
164
7
310
293
81
428
79
4
Port Heiden
Port Moller
ALASKA PENINSULA
Unimak Is.
Shumagin Islands
Unalaska Is.
PACIFIC OCEAN
170°
165°
160°

FIGURE 9. Number of male king crabs tagged and released, by area, 1955–61.

TABLE 6. Adult male king crabs tagged at locations in the station grid[1], 1955–61, by region.

	No. of crabs by year								
Region[2]	1955[3]	1956[3]	1957	1958	1959[4]	1960	1961[4]	Total	Percent
I	—	—	—	—	—	15	324	339	2.3
II	—	—	—	—	—	6	13	19	0.1
III	144	165	272	1,582	790	291	1,018	4,262	28.4
IV	—	—	152	532	641	242	329	1,896	12.7
V	57	—	49	757	—	105	60	1,028	6.9
VI	791	403	263	762	954	252	529	3,954	26.4
VII	160	100	199	925	204	318	—	1,906	12.7
VIII	199	257	107	609	205	88	16	1,481	9.9
IX	—	—	26	59	—	11	—	96	0.6
Total	1,351	925	1,068	5,226	2,794	1,328	2,289	14,981	100.0

[1] See Figure 4.

[2] See Figure 5.

[3] Tagging was done only in the vicinity of the commercial fishery (Figure 4).

[4] No tagging done east of Port Moller (Figure 1).

crabs in the various regions were obtained by analyzing the distribution of the male crabs tagged at stations in the grid in 1955–61 (Table 6). In each year the duration of tow at each station was uniform, the stations were spaced at equal intervals, and all viable male crabs caught were tagged and released. Only in 1957, 1958, and 1960, however, were tagging stations in the grid extended throughout the area presumed to include the significant distribution of male king crabs. In 1955–56, crabs were tagged only in the immediate vicinity of the commercial fishery; in 1959 and 1961, inclement weather and other factors prohibited tagging east of Port Moller (Figure 1). Because of the uniformity of sampling and tagging procedures in 1957, 1958, and 1960, the percentage of crabs tagged in each of the nine regions during these years was assumed to represent the relative abundance of crabs at the time of sampling (Figure 10). To show the selectivity of the king crab fishery, the percentage distribution of the commercial catch by region (Japan and United States only) in 1955–60 is also shown.

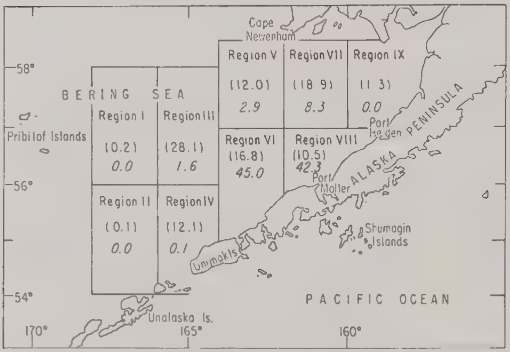

FIGURE 10. Distribution of 7,622 male king crabs tagged at grid stations in the eastern Bering Sea, 1957, 1958, and 1960, and distribution of the commercial catch (Japan and United States only), 1955–60. Upper numbers in parentheses indicate percent of total tagged king crabs, 1957, 1958, and 1960. Lower numbers indicate percent of commercial king crab catch (Japan and United States only), 1955–60.

Regions in which the larger numbers of adult male crabs were tagged were not the regions accounting for the largest portions of the commercial catches. Regions VI and VIII, where 27.3 percent of the tagged crabs were released (Figure 10), accounted for 87.3 percent of the commercial catch, while in Regions III, V, and VII the percentages of tagged crabs and commercial catch were 59.0 and 12.8, respectively. The discrepancy between the relative abundance of adult male king crabs and the commercial catch in the different regions was the result of the fishery's preference for crabs that had not molted during the past year, the so-called " old-shelled crabs ", as opposed to crabs that had molted during the past year, the " new-shelled crabs ". A third group of crabs judged not to have molted during the past two years, the " very old-shelled crabs ", was also acceptable for commercial processing. " Soft-shelled crabs ", individuals which may have molted only in the past few days, were extremely rare in the catches taken for tagging, and they do not appear at all in the commercial catch. Male crabs of the various shell conditions were not distributed uniformly throughout the eastern Bering Sea, and the commercial fishery tended to concentrate in areas of abundance of the more desirable crabs.

Although new-shelled crabs composed three-fourths

Table 7. Shell condition at time of release of male king crabs tagged at grid stations, 1955–61.

Shell condition	Percentage by region of release[1]									All regions
	I	II	III	IV	V	VI	VII	VIII	IX	
Soft	—	—	0.1	0.2	—	0.3	0.1	0.3	—	0.2
New	98.5	100.0	88.8	73.0	81.6	70.7	71.2	52.6	74.0	76.2
Old	1.5	—	8.7	20.7	8.7	21.2	13.3	34.8	18.7	16.3
Very old	—	—	2.4	6.1	9.7	7.8	15.4	12.3	7.3	7.3
Number released	339	19	4,262	1,896	1,028	3,954	1,906	1,481	96	14,981

[1] See Figure 5.

Table 8. Shell condition at time of recovery of male king crabs tagged at locations in the station grid, 1955–61.

Shell condition	Percentage by region of recovery[1]									All regions
	I	II	III	IV	V	VI	VII	VIII	IX	
Soft	—	—	—	—	—	—	6.7	—	—	—
New	—	—	22.6	8.3	50.0	3.0	16.7	1.2	—	8.0
Old	—	—	75.9	71.7	41.7	86.8	73.3	79.6	100.0	81.2
Very old	—	—	1.5	20.0	8.3	10.2	3.3	19.2	—	10.8
Number recovered	—	—	574	67	17	1,024	79	653	8	2,422

[1] See Figure 5.

Table 9. Rate of return from tagged king crabs released at grid stations, 1955–61.

Region of release[1]	Releases		Returns		
	Number	Percentage of total crabs tagged	Number	Rate of return	Percentage contribution to fishery
I	339	2.3	77	22.7	3.2
II	19	0.1	3	15.8	0.1
III	4,262	28.4	828	19.4	34.2
IV	1,896	12.7	253	13.3	10.4
V	1,028	6.9	117	11.4	4.8
VI	3,954	26.4	660	16.7	27.2
VII	1,906	12.7	241	12.6	10.0
VIII	1,481	9.9	234	15.8	9.7
IX	96	0.6	9	9.4	0.4
Total	14,981	100.0	2,422	16.2	100.0

[1] See Figure 5.

of all crabs tagged at grid stations (Table 7), they were not suitable for processing during spring and summer because of their low meat content and poor quality. The amount of meat recovered during spring and summer from a new-shelled crab is only about two-thirds of the amount recovered from an old-shelled crab (INPFC Annual Report 1960, p. 118). By fall, however, the meat content of new-shelled crabs is sufficiently improved for them to be acceptable.

New-shelled crabs were more numerous than those of the other three groups in all regions of the eastern Bering Sea, but the percentages in the offshore regions were consistently greater than in the inshore regions adjacent to the Alaska Peninsula (Table 7). Old-shelled crabs were in greater proportions in the inshore regions. Of the total number of crabs tagged at the grid stations, 16 percent were old-shelled and 7 percent were very old-shelled. Of the tagged crabs recovered by the commercial fishery, more than 80 percent were classified as old-shelled and 11 percent as very old-shelled at the time of recovery (Table 8). Crabs of these two classifications constituted over 97 percent of the tagged crabs recovered in the most heavily exploited regions—VI and VIII. Only 8 percent of the tagged crabs in the commercial catch were classified as new-shelled crabs, and more than half of these were recovered in the fall offshore fishery in Region III.

Of the total number of crabs released at grid stations and eventually recovered, the proportion of tagged crabs contributed by any region of release was assumed to be a measure of the extent to which the region contributed crabs to the commercial fishery (Table 9). Returns of crabs tagged in each region were essentially in direct proportion to the number of releases in each region. Consider, for example, the 339 tagged king crabs released in Region I. These crabs comprised 2.3 percent of the total releases at grid stations. A total of 77 of these were returned by the commercial fishery—3.2 percent of the total of 2,422. The general

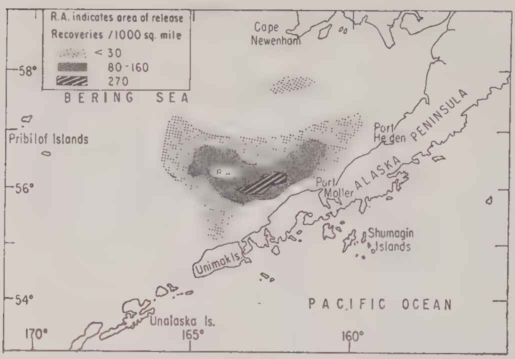

FIGURE 11. Dispersion of 1,086 male king crabs recovered from a total of 11,000 tagged at one location in 1957.

TABLE 10. Number of returns, by region, of king crabs tagged at one location[1] in 1957.

Region of recovery[2]	No. of returns by year							
	1957	1958	1959	1960	1961	1962	1963	Total
III	35	1	11	3	53	55	72	230
IV	0	0	0	3	2	1	9	15
V	0	0	0	0	1	0	0	1
VI	0	107	151	115	73	114	50	610
VII	0	0	4	0	0	0	0	4
VIII	0	31	14	45	59	41	35	225
IX	0	0	0	0	0	1	0	1
Total	35	139	180	166	188	212	166	1,086

[1] See Figure 11 for location of release.

[2] See Figure 5.

agreement between the percentage of total crabs tagged (column 3) and the percentage contribution to the fishery from each region (column 6) as well as the rate of tag return (ranging from 9.4 to 22.7 percent; mean, 16.2 percent) suggested that each release region contributed a relatively equitable proportion of crabs to the commercial fishery. The two release regions with the highest rates of return (I and III) supported almost no commercial fishing; the tagged crabs released there were recovered in other regions. It is apparent that the fishery was effective in taking crabs released over the entire eastern Bering Sea.

MOVEMENT OF TAGGED KING CRABS

The wide dispersion of crabs from a locality was illustrated by the tagging of large numbers of crabs from a single concentration in the summer of 1957. This group of crabs was located in Regions III and VI, about 80 miles north of Unimak Island (Figure 11). A buoy was anchored to mark the location, and repeated trawl hauls were made around the site. Altogether 11,000 male king crabs were tagged. In 1957–63, the commercial fishery returned 1,086 of these crabs (Table 10). The largest numbers of returns came from areas where fishing was concentrated.

A detailed review of release-recovery data by combinations of such factors as year of release, year of recovery, sizes at release or recovery, and shell condition revealed no definite pattern of movement except generally away from the point of release.

MIGRATION

Tagging data offered little information on the within-year movement of king crabs because tagging took place during or after the commercial season; little time was available for appreciable movement from point of release between date of tagging and cessation of commercial fishing. In 1961, for example, tagging began in July and commercial fishing began in April and extended through October. A total of 55 crabs released in 1961 were recovered in the fishery, of which 51 were retrieved within 30 miles of the point

TABLE 11. Number of returns (1955–63) of tagged male king crabs released in 1955–61, by regions of release and recovery[1].

Region of release	No. of returns by region of recovery									
	I	II	III	IV	V	VI	VII	VIII	IX	Total
I	—	—	36	5	—	23	—	13	—	77
II	—	—	2	—	—	1	—	—	—	3
III	—	1	520	47	2	862	15	324	4	1,775
IV	—	—	152	25	1	200	1	53	—	432
V	—	—	36	1	8	202	9	210	1	467
VI	—	—	196	18	5	638	27	288	5	1,177
VII	—	1	24	2	4	92	29	163	2	317
VIII	—	—	18	5	4	68	20	207	—	322
IX	—	—	1	—	—	7	—	7	—	15
Total	—	2	985	103	24	2,093	101	1,265	12	4,585

[1] See Figure 5.

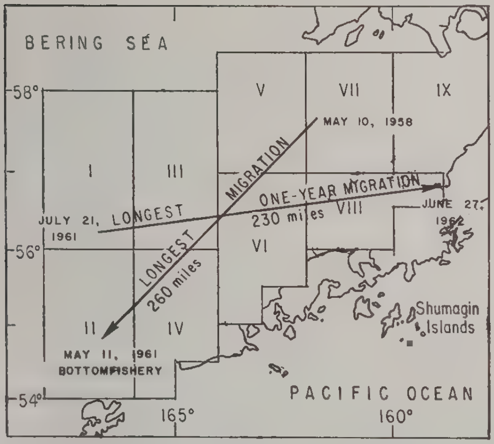

Figure 12. Greatest distances traveled by tagged king crabs.

of release. Two factors adversely affect the usefulness of such information for studying seasonal migration: (1) the location of tag recovery was reported as the noon position of the factoryship, instead of the position where the catcher boat actually lifted the tangle net, and (2) inclement weather as well as positioning of LORAN stations make it difficult to determine precisely the locations of release and recovery.

Mixing of Tagged Crabs in the Commercial Fishery

Adult male king crabs dispersed widely. With few exceptions, some crabs from every region of tag release were recaptured in each of the regions in which fishing vessels operated (Table 11). This mixing of tagged crabs among the regions suggests that the king crabs of the eastern Bering Sea constituted a single population, in which individuals move and mix randomly.

Distances Traveled

About 50 percent of the tag returns were from crabs recaptured within 50 nautical miles of the release position, and 90 percent were from crabs recaptured within 100 miles. Four crabs were recovered more than 200 nautical miles from their locality of tagging.

The greatest distance between position of release and recovery was 260 miles. This crab was at large three years and had been released about 60 miles south of Cape Newenham (57°58′N, 161°30′W); it was recovered 45 miles north of Unalaska Island (54°47′N, 166°12′W) by a Japanese bottomfishing vessel (Figure 12).

The longest " distance traveled " by a crab during a single year was 230 miles. This crab was tagged July 21, 1961, near the western limit of the station grid (56°19′N, 166°24′W), and was recovered June 27, 1962, about 40 miles west of Port Heiden (56°51′N, 159°55′W) (Figure 12).

Rates of movement were estimated from tagged crabs released and recovered during the same fishing season. The accuracy of such information, however, is influenced by discrepancies between the true recovery position (where the crab was taken by the catcher boat) and the reported recovery position (noon position of the factoryship). Rates of movement, calculated from straight-line distances and numbers of days between release and recovery, for 247 crabs ranged from 0 to 11 miles per day and averaged 0.36 miles. The average distance traveled per day was similar for new-shelled and old-shelled crabs.

GROWTH AND SIZE AT RECRUITMENT

Large male king crabs are deliberately selected by the commercial fishery by (1) scouting, (2) use of mesh sizes in tangle nets that favor the retention of the larger animals, and (3) sorting of the catch by fishermen, who return females and under-sized males to the sea. Growth of male king crabs and their size at recruitment into the commercial fishery were determined by contrasting length distributions at release and recovery of groups of crabs at liberty for the same number of years. Of the 4,585 tags considered, 4,384 had complete data on size and date of recovery; numbers returned after different periods at liberty were as follows:

Years at liberty	Nos. returned with usable data
0	247
1	923
2	897
3	691
4	703
5	599
6	303
7	21
Total	4,384

Length frequencies within each group were constructed from measurements taken at time of release and at time of recovery. All of the frequency distributions were unimodal and, as was to be expected, the length modes at release differed from the length modes at recovery (Figure 13). The difference between modal length at release and modal length at recovery, within any group, gives an approximation of growth in the period between tagging and recovery.

The modal length at time of release was 16 cm for crabs at liberty for one year, 15 cm for those at liberty for two years, 14 cm for those at liberty for three years, etc.; modal size decreased by 1 cm from one group to

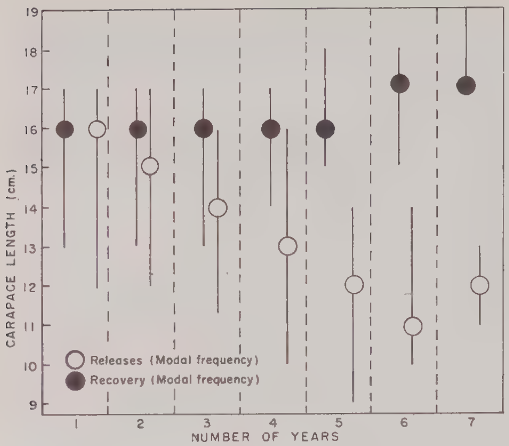

FIGURE 13. Modal lengths of tagged king crabs at release and recovery, by number of years at liberty. Lines include 10–90 percentile range.

the next, consecutively to the sixth group, in which crabs at liberty for six years had a modal length of 11 cm at time of tagging.

Modal lengths of crabs at time of recovery remained near 16 cm for each of the groups; i.e., the size at recovery was uniform regardless of the number of years the crabs had been at liberty. Only in the groups of crabs at large for six and seven years did the modal size at time of recapture increase to 17 cm.

Nearly 80 percent of the tagged crabs recovered had carapace lengths greater than 15 cm and 30 percent were larger than the modal length of 16 cm. The largest tagged crabs recovered were 20 cm in carapace length. The selectivity of the commercial fishery for the larger crabs is demonstrated by the fact that less than 3 percent of the recovered tagged crabs were smaller than the " regulatory " minimum width of 13 cm (or an equivalent carapace length of 11 cm), even though about 30 percent were smaller than 11 cm in carapace length at time of release.

Data on recruitment size and growth may be summarized as follows:

1. The commercial fishery was selective for crabs having a carapace length of 16 cm or greater.
2. The carapace length at which crabs were first recruited into the commercial fishery was about 13 cm.
3. The mean growth rate of adult male king crabs was about 1 cm per year.[1]

SUMMARY

1. To study factors which affect the yield to the commercial fishery, 32,214 male king crabs were tagged in the eastern Bering Sea in 1955–61; 4,687 tags (14.5 percent) were returned in 1955–63 by the fisheries of Japan, the United States, and the Soviet Union. Only tags for which the exact recovery position was given (4,585, or 14.2 percent) were considered in the report.

2. Tubular plastic " spaghetti " tags which pass through the arthral muscle were used because they remain with the crab throughout molting.

3. Tagging locations were of two types: (1) stations at predetermined positions on a rectangular grid, at 20-mile intervals; and (2) stations in areas of known crab abundance. About equal numbers of crabs were tagged at each type of release location. Crabs for tagging were captured by otter trawl.

4. The rate of return of crabs tagged in 1955 through 1960 ranged between 12 and 17 percent; a 22 percent rate of return for crabs tagged in 1961 occurred in 1961–63, in spite of the fact that U.S.S.R. tag recoveries had not been received.

5. The eastern Bering Sea was arbitrarily divided into nine regions of tag release and recovery. By region of release, the proportions of tagged crabs returned by the commercial fishery ranged from 9.4 to 22.7 percent.

6. No tagged crabs released in the eastern Bering Sea were returned from the Pacific Ocean. The male king crabs of the eastern Bering Sea and the northern Pacific Ocean appear to be separate stocks.

7. The western and northern limits of the distribution of adult male king crabs in the eastern Bering Sea were about 168°W and 58°30′N, respectively; the southern and eastern limits were the shores of the Alaska Peninsula and Bristol Bay.

8. Recoveries by the commercial fishery of crabs tagged at grid stations were essentially in direct proportion to the number of releases in each region. The fishery was effective in taking crabs released in all regions of the eastern Bering Sea.

9. New-shelled male crabs predominated in all of the regions. They constituted more than 75 percent of crabs released at grid stations. The proportion of new-shelled to old-shelled and very old-shelled crabs was greatest in the offshore regions. Fishing grounds appear to be determined by the availability of old-shelled and very old-shelled male crabs. Although old-shelled and very old-shelled crabs comprised only 24 percent of the crabs tagged, these groups made up more than 80 percent of tagged crabs recovered in the commercial fishery. New-shelled male crabs, although the most abundant form in the eastern Bering

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[1] Weber and Miyahara (1962) reported an average length increase of 1.6 cm per molt for adult male king crabs of the eastern Bering Sea. Since many of the larger crabs do not molt annually, an average annual growth of 1 cm appears to be reasonable.

Sea, constituted less than 8 percent of the tagged crabs taken commercially.

10. Tagged crabs dispersed widely from the region of release, and with few exceptions all regions of release were represented in the commercial catches made in the various regions of recovery. This mixing suggested that the king crabs of the eastern Bering Sea constitute a single population.

11. The greatest " distance traveled " by a king crab in a single year was about 230 nautical miles. A crab at liberty for three years was recovered 260 nautical miles from its point of release. About 50 percent of the recoveries were within 50 miles of the release position, and 90 percent were within 100 miles.

12. The modal length of tagged crabs at recovery was 16 to 17 cm. Nearly 80 percent of the tagged crabs recovered had carapace lengths greater than 15 cm, and fewer than 3 percent were smaller than 11 cm. The average growth of tagged male king crabs was about 1 cm per year between time of release and time of recovery.

ACKNOWLEDGMENTS

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Erythrocyte Antigens and Natural Isoagglutinins of the American Eel, *Anguilla rostrata*, from Chesapeake Bay

Carl J. Sindermann and George E. Krantz

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Erythrocyte Antigens and Natural Isoagglutinins of the American Eel, *Anguilla rostrata*, from Chesapeake Bay

CARL J. SINDERMANN AND GEORGE E. KRANTZ
U. S. Department of the Interior
Fish & Wildlife Service
Bureau of Commercial Fisheries
Biological Laboratory, Oxford, Maryland 21654

ABSTRACT: Blood of American eels from Chesapeake Bay was examined with serological techniques. Individual variations in erythrocyte antigens were disclosed by natural isoagglutinins in eel sera and by agglutinins in absorbed rabbit antisera. The complexity of the isoantigen-isoagglutinin system seems to exceed that presently known for any other vertebrate.

Introduction

One of the most fascinating series of studies in marine biology concerns the systematics, life histories, and migrations of Atlantic eels. Early definitive work published by Schmidt (1914, 1915, 1922, 1925, 1935) and Ege (1939) provided evidence for the existence of two species: *Anguilla rostrata* (LeSueur) found on the Atlantic coast of North America, and *Anguilla anguilla* (L.) from the coast of Europe. Larval collections indicated that both species spawned in overlapping areas of the Sargasso Sea, even though no ripe eels or eggs were found. Tucker (1959) re-examined Schmidt's data and proposed the alternate hypothesis that American and European eels were merely ecophenotypes of the same species, with a common spawning location. Reaction to Tucker's proposal was immediate, strong, and somewhat subjective (D'Ancona, 1959; Jones, 1959; Deelder, 1960; Bruun, 1963) but no new data were presented. Vladykov (1964) pointed out that Schmidt's data fail to establish the breeding place of the American eel, and that the spawning area may be much further south than the Sargasso Sea area described by Schmidt.

A number of attempts have been made recently to provide biochemical-serological information that might bear on the problem created by Tucker's alternate hypothesis. Gemeroy and Boyden (1961) used a precipitin test with serum proteins of American and European eels. This technique, however, does not entirely eliminate possible environmental influences. Sick *et al.* (1962) initially found no differences in hemoglobin electrophoretic patterns or chromosome numbers between American and European eels. A later study of much larger samples (Sick *et al.*, 1967), however, did disclose the existence of three hemoglobin types in American eels, suggesting the presence of a rare allele in American eels that is absent in European eels. Electrophoretic studies of eel serum (Fine *et al.*, 1964, 1965; Drilhon *et al.*, 1966) disclosed the existence of three transferrin types in European eels, and a subsequent study (Fine *et al.*, 1967) reported marked differences in frequencies of these types in European and American eels.

One possible source of definitive genetic data that has not been explored involves the techniques of blood grouping. Studies of erythrocyte antigens and the establishment of blood group systems in fishes have progressed greatly during the past decade (Sindermann and Mairs, 1959, 1961;

Sprague and Vrooman, 1962; Ridgway, 1962; Cushing, 1964). Limited genetic information (Hildemann, 1956, 1962; Sindermann and Mairs, 1961; Ridgway, 1962, 1966; Utter and Ridgway 1966) and extrapolation from comparable studies of higher vertebrates (Stormont, 1961) indicate that blood group antigens of fishes are genetically determined.

Investigation of erythrocyte antigens of the eel, description of blood group systems, and subsequent determination of antigen and gene frequencies in eels from different geographic locations on both sides of the Atlantic could provide information about the degree of genetic similarity or dissimilarity. It was with this thought in mind that we began in 1962 the exploratory work reported in this paper. The data presented here establish that individual variations exist in erythrocyte antigens of American eels; that a number of isoagglutinins for their detection are present in eel serum; and, most importantly, that antigens detectable with absorbed rabbit antisera can be categorized for quantitative studies. As yet no quantitative studies of antigen frequencies in American and European eels have been undertaken.

Methods

Eels with an average length of 50 cm were obtained from the Tred Avon River, a tributary of Chesapeake Bay, in water with salinity of approximately 15‰. Blood was obtained by heart puncture, allowed to clot, and stored in the refrigerator overnight. Serum was then decanted. Cells were washed from clots, washed twice in 1.5% saline, and prepared as approximately 4% suspensions in 1.5% saline. Repeated bleedings of individual tagged eels were possible. Cross-reactivities of sera and cells were tested by tube agglutination using 0.2 ml of serum diluted 1:1 with 1.5% saline and 0.05 ml cell suspension. Tubes were read after 24-hour refrigeration at 4C and 1-minute centrifugation at approximately 1000 rpm. Presence and degree of agglutination were recorded conventionally as follows: (++++) complete agglutination with a single consolidated pellet; (+++) strong agglutination with several large clumps; (++) moderate agglutination with numerous smaller clumps; (+) weak agglutination with many very small clumps visible macroscopically; and (−) no agglutination. Saline controls were used throughout. Absorptions of reactive eel sera, to remove certain isoagglutinins selectively, involved addition of undiluted serum from one fish to packed washed cells from another fish in 4:1 proportions. The cell-serum suspension was incubated for 30 minutes at room temperature with occasional agitation, centrifuged, and the absorbed serum decanted for use in cell agglutination tests. One such absorption usually removed agglutinins reactive with the absorbing cells, but usually left antibodies reactive with cells from other individuals.

Rabbit antisera were produced against cells of individual eels by six intraperitoneal injections of 1 ml of a 50% suspension of washed eel cells given on alternate days. Rabbits were bled 7, 10, 14, and 17 days after the last injection and the antisera frozen in 5 ml aliquots until used. Antisera were incubated at 56 C for 30 minutes just before testing, to destroy complement activity.

Antiserum absorptions—which constitute a fractionation method to produce specific reagents—involved addition of rabbit antiserum (diluted 1:10 with 1.5% saline) to packed washed cells from individual eels in proportions of 1 part cells to 4 parts antiserum. The cell-antiserum suspension was incubated 60 minutes at 37 C, centrifuged, and the absorbed antiserum decanted and tested at 1:4 dilution. One such absorption was usually sufficient to remove all antibodies reacting with the absorbing cells but normally left antibodies capable of reacting with cells from other individuals.

Tests by tube agglutination were made with 0.2 ml diluted absorbed antiserum and 0.05 ml cell suspension. Readings were taken after 30-minute incubation at room temperature and 30-second centrifugation at approximately 1000 rpm. Presence and degree of agglutination were recorded as described above.

Isoagglutination

Cross-matches of cells and sera provided clear indication of the presence of strong isoagglutinins in eel sera and of antigenic diversity in eel erythrocyte antigens, as can be seen in Table 1, which includes the results of a sample cross-match panel. Cells of most eels tested possessed antigens reactive with some sera, and, in certain individuals, with most of the sera used. As examples of the broad range of reactions, the serum of eel 7 possessed agglutinins for the cells of all other eels in the panel, whereas the serum of eel 5 possessed weak agglutinins for only three of the eels in the panel. Red blood cells of eels 5, 6, and 7 were reactive with most of the sera in the panel, but the cells of eels 3, 8, and 10 were reactive with only a few.

Table 1. Cross-matches of erythrocytes and sera of American eels.

Serum	Cells									
	1	2	3	4	5	6	7	8	9	10
1	−	+	−	−	+	++	+	−	−	−
2	−	−	−	−	+	++	−	−	+	−
3	−	−	−	+	++	++	++	−	++	−
4	+	++	−	−	+	+	+	−	−	+
5	+	−	−	−	−	−	+	+	−	−
6	−	−	−	+	+	−	+	−	−	−
7	+	++	++	++	++	+	−	+	+	+++
8	+	−	−	+	−	++	+	−	−	−
9	+	++	−	++	+	++	+	−	−	+
10	−	+++	+	++	++	+	++	+	+	−

Table 2. Examples of results of tests with eel erythrocytes and absorbed eel sera.

Serum	Absorbing Cells	Test Cells									
		1	2	3	4	5	6	7	8	9	10
5	8	++	−	−	−	−	−	−	−	−	−
7	9	−	+	++	−	−	+	−	−	−	+
9	7	++	++	−	+	−	+	−	−	−	−

Table 3. Reactions of eel erythrocytes with absorbed rabbit antisera.

	Eel cells									
	11	12	13	14	15	16	17	18	19	20
Rabbit H2 absorbed with cells of eel 668	+	+	+	+	+	+	−	−	−	+
Rabbit G2 absorbed with cells of eel 668	−	+	−	−	+	+	−	−	−	−

Indication of the complexity of the eel cell antigens was found by absorbing reactive sera with selected cell samples and then retesting with other cells in the panel. Examples of reactions obtained are presented in Table 2. Absorptions of reactive sera removed agglutinins for the absorbing cells, but left agglutinins reactive with cells of most other individuals. For example, the serum of eel 9 was reactive with cells of seven other eels in the panel before absorption. It was still reactive with cells of four eels after absorption with cells of eel 7, despite the fact that the cells of eel 7, as seen in Table 1, possessed antigens reactive with most of the sera in the panel. A number of other test panels were set up, with a total number of eels in excess of 100. Thus far we have not found two eels that gave an identical pattern of reactions in any panel.

Antiserum Absorptions

Antisera prepared in rabbits by injections of erythrocytes from individual eels were absorbed with cells of other individual eels. Most of the antisera were found to contain only species specific antibodies when absorbed with erythrocytes of individual eels. However, two antisera absorbed with cells of one eel gave complementary results, since test cells from other eels reacted with both, or one, or neither reagent (Table 3). Unabsorbed rabbit antisera agglutinated all eel cells, with a +++ or ++++ reaction.

By use of these absorbed reagents, it is possible to type eels for possible quantitative studies. As might be expected, the antigenic complexity apparent in cross-matches described in the previous section is not apparent when using rabbit antisera. Certain of the erythrocyte antigens of the eel undoubtedly provoke stronger immune response than others in the rabbit, thereby masking some of the antigenic complexity.

Discussion

One approach to the problems of Atlantic eel taxonomy and migrations is blood grouping; subpopulation analyses of several commercially important fish species such as sardines, tuna, and salmon have been based on such immunogenetic studies. Antisera prepared in mammals or birds, or natural sera from mammals, have been most widely used, although isoagglutinins are known to exist in some fishes. American eels differ from any other teleost studied thus far in the complexity of isoantigens detectable by natural isoagglutinins. As opposed to the relatively simple isoantigen-isoagglutinin systems involving no more than two antigens, described for other teleosts and elasmobranchs (Cushing and Durall, 1957; Sindermann and Mairs, 1961; Sindermann and Honey, 1964), it appears that each individual eel may have antigenic specificities, as detectable by isoagglutination, differing from all other eels —or that the observed reactions involve a number of antigens in many combinations. Our cross-matches, for example, have included over 100 eels, but we have not seen an identical pattern of agglutination with the cells of any two individuals in our cross-match panels.

Individual variations have been reported in erythrocyte antigens and serum agglutinins of Japanese eels, *Anguilla japonica* Temminck and Schlegel. Sugishita (1935) found individual variability in sera of Japanese eels in their ability to agglutinate human erythrocytes. Suyehiro (1949) reported isoagglutination in the same species. He found weak positive reactions in 11 of 200 combinations of cells and serum, and doubtful agglutinations in another 8. These reactions included two autoagglutinations. Although such anomalous reactions may be significant, they were not discussed further by Suyehiro. We have observed in our work that contamination of eel serum by mucus or tissue fluids, as frequently happens when blood is collected without sufficient care, can produce autoagglutination. As pointed out by Cushing (1964), the observations of Sugishita and Suyehiro have not been extended by others to the point of establishment of eel blood group systems.

Isoagglutinin titers of American eels from Chesapeake Bay seem much higher than those reported by Suyehiro for Japanese eels. Using a 1:1 proportion of undiluted serum and 2% cell suspensions in cross-matches, he obtained weak positive or doubtful reactions in only a few of the combinations; titers in the present work with American eels reached 1:32, and strong positive reactions were obtained in many combinations with a final 1:4 serum dilution. Temperature may play a role, since tests of American eels from the Maine coast disclosed fewer and weaker agglutinations than were found for samples from Chesapeake Bay. Maximum summer sea water temperatures are more than 10 C cooler on the Maine coast than in Chesapeake Bay.

Isoimmunization followed by absorption analysis would be a logical expansion of the present work. Studies with higher vertebrates have demonstrated the utility of this approach, and examples of successful production of isoimmune agglutinins in fish have been published by Hildemann (1956), Ridgway and Klontz (1960), and Ridgway (1962, 1966). Temperature is an important factor in antibody production in fishes; the ability of tagged eels to survive well in environmental water temperatures of 25 C—demonstrated in our studies—should facilitate isoimmunization experiments.

Conclusions

American eels differ from other teleosts studied to date in the complexity of their natural isoagglutinin-isoantigen systems. Relatively simple systems are found in other teleosts or elasmobranchs—usually no more than two antigens are reactive with their respective isoagglutinins. Eels appear to possess a number of antigens in various combinations, almost to the point where each individual fish has an antigenic identity, as disclosed by isoagglutinins, different from other individuals. The apparent complexity of the natural isoagglutinins of eels and the possible influence of temperature on their titers suggest that eels might provide a model system for fundamental studies of the nature and role of serum isoagglutinins in the vertebrates.

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Northwest Atlantic Herring Catch Zooms

Total 1967 Landings Topped Billion Pounds For First Time

By Bernard E. Skud and John E. Watson
Bureau of Commercial Fisheries Biological Laboratory

BOOTHBAY HARBOR, ME. – The catch of Atlantic herring along the North American Coast has increased explosively in the past two years, and in 1967 totaled over 1 billion lbs. Seven countries participated in the catch, and the fishery extends from Newfoundland to Virginia.

The fishery began its rapid growth in 1961. Before then, only the United States and Canada exploited the North American herring resource, and the yearly catch averaged less than 400 million lbs. The fish were processed for sardines, meal and oil, salting, bait and for pearl essence.

The Russians began fishing for herring on Georges Bank in 1961, and landed over 350 million lbs. in 1962.

In subsequent years Poland, West Germany, East Germany and Romania entered the fishery, and the fishing grounds were expanded in Nova Scotia, in the Gulf of Maine and, most recently, in waters south of Cape Cod.

The herring landings by all countries ranged from 400 to 700 million lbs. in 1962-65; exceeded 900 million lbs. 1966; and reached 1.3 billion lbs. in 1967.

The catch by country is summarized in the accompanying table. Canada and Russia accounted for 80% of the catch in 1967. Nearly all of the catch by Canadians, which doubled from 1964 to 1967, is within their territorial waters, but in the past two years Canadians have fished in international waters off the Maine coast and on Georges Bank.

The other countries have concentrated in international waters along the Maine coast, on Georges Bank, in the Gulf of Maine and off Long Island, N. Y. The 1967 catch, in other than Canadian waters, exceeded 500 million lbs.

North American Catch (in millions of pounds) of Atlantic Herring‡

Nation	1960	1961	1962	1963	1964	1965	1966	1967
Canada	246	188	246	252	311	403	565	761
Germany	—	—	—	—	—	—	—	57
Poland	—	—	*	*	*	3	28	84
Romania	—	—	—	—	—	—	7	*
Russia	—	149	354	221	294	93	270	280
U.S.A.	155	59	158	155	62	76	74	71
Other	—	—	—	—	*	4	8	37
Total	401	396	758	628	667	579	952	1290

‡The statistics are derived from reports of the International Commission for Northwest Atlantic Fisheries. Asterisk (*) indicates catch less than 1 million pounds.

The U.S. share was 71 million lbs., mostly taken in coastal Maine for use in the sardine industry. The U.S. catch has exceeded 150 million lbs. in three of the years since 1960, but its maximum catch, nearly 200 million lbs., was taken in 1948.

Other nations, particularly Japan and the Netherlands, have shown an interest in the fishery, and may join the herring fleets.

The major portion of the U.S. catch is used for sardine canning, but other uses are the basis for important industries in Maine. Fish meal and oil production have increased, and companies in the southern New England states have recently added to this production. Greater use of purse seines has been the impetus for this development.

The pearl essence industry which is centered in eastern Maine is another user of herring. The herring scales and other body parts contain the pearl essence that is used in the manufacture of a variety of products, ranging from paints to cosmetics.

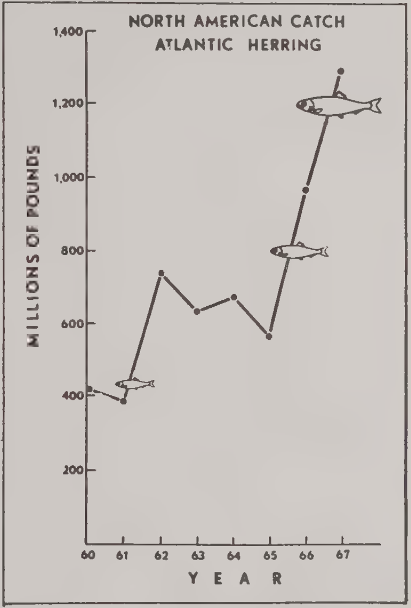
PURSING POPULAR

Herring are also used as bait in the lobster fishery.

Most of the U.S. catch in past years has been taken with stop-seines and weirs, but purse seines have been gaining popularity and in 1967 over-shadowed the traditional methods by accounting for 57% of our catch. This trend toward purse seine fishing has been much stronger in Canada; over 70% of their catch is taken in this manner.

In contrast, the Russians and other foreign nationals rely primarily on bottom and midwater trawls for their catches. In the first few years of the Russian fishery, gillnets were used as well, but they have since given way to trawls.

To safeguard its fishing industries, the United States maintains membership in the International Commission for Northwest Atlantic Fisheries (ICNAF) and is represented at the annual meetings along with the other member nations: Canada, Denmark, France, Germany, Iceland, Italy, Norway, Poland, Portugal, Romania, Russia, Spain and the United Kingdom. Through this organization, the member nations exchange information and consider measures to protect and preserve the international fisheries. Catches, fishing gear and biological research are openly discussed.



DOUBLED AND TRIPLED, **the Atlantic herring fishery off North America has seen fast growth during the 1960s.**

Herring studies in the U. S. originate at the Bureau of Commercial Fisheries Biological Laboratory here in Boothbay Harbor. The U. S. scientists have been especially concerned with the valuable inshore herring fishery which centers in Maine; but with the opening of a fishery in nearby international waters they have extended their work offshore to determine the effect of fishing on these stocks and to provide for potential American interests.

The Boothbay Harbor Laboratory, which gets first-hand knowledge by placing research teams on the fishing grounds, has shown that the offshore stocks are independent of those fished in the coastal waters. This information is important for the Maine sardine industry and may encourage a greater exploitation of the offshore herring stocks by other segments of the U.S. industry.

Until now, the U.S. has not been quick to take advantage of this expanding fishery, but catch records through September 1968 indicate that U. S. industries have increased their efforts to obtain a greater share in this valuable resource.

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Replacement of Rostral Teeth in Sawfishes and Sawsharks

Bob H. Slaughter and Stewart Springer

In recent sawfishes, *Pristis* (order Batoidei), rostral teeth that are lost are not replaced and those not severely damaged in use increase in size throughout life. Presumably similar conditions pertain to fossil sawfish genera having socket-like attachments for rostral teeth. In recent sawsharks, *Pristiophorus* and *Pliotrema* (order Selachii), rostral teeth are replaced if lost and do not increase in size after reaching a functional position. Similarities in tooth development and the process of replacement were observed in recent sawsharks (Selachii) and in the Cretaceous sawfish genus *Sclerorhynchus* (Batoidei). Also, the pattern of varying length of rostral teeth in adults of recent sawsharks (Selachii), which is explained by the appearance of both new and replacement teeth at intervals during growth, offers a possible explanation for the presence of rostral teeth of various lengths in the Cretaceous ganopristid sawfish *Onchopristis numidus* (Batoidei).

Introduction

The number of rostral teeth in recent sawfishes (Batoidei) remains constant throughout life unless teeth are damaged and lost through accident; lost rostral teeth are not replaced. The number of teeth has limited usefulness as a taxonomic character for the identification of species in the single present day genus *Pristis*. The teeth are firmly embedded in socket-like cups in the rostrum (Fig. 1) and are perpendicular to the axis of the rostrum throughout development and growth.

Rostral teeth of *Pristis* are stout, and very few losses are evident in a sample of 18 large dry saws in the U. S. National Museum collections. Rostral teeth in the larger, and presumably older specimens, show considerably more wear near their tips (Fig. 2) than do teeth of half-grown examples. Splintering appears to have occurred frequently in rostral teeth from our large specimens; the cleavage is such, however, that the damaged teeth often remain pointed but slightly shorter than neighboring teeth. When splintering has not occurred, the teeth in *Pristis* are of nearly uniform length (except for those at the tip and near the base of the rostrum).

It has long been known that in sawsharks (Selachii) the number of rostral teeth increases as the shark grows, and the irregularity in length of teeth is less noticeable in the young than in older specimens (Garman, 1913). Both *Pristiophorus* and *Pliotrema* show a tendency to form a regular pattern of short, intermediate, and long teeth in repetitive series, but in the literature we have found neither mention of the process involved in the sawshark's tooth development nor an explanation for the variation in length of rostral teeth.

Schaeffer (1963) called attention to considerable variation in the size of teeth attached to the calcified rostrum of the Cretaceous ganopristid sawfish *Onchopristis numidus* (Stromer). He suggested some form of heterochronic eruption of the teeth but added that no method was known whereby such teeth could be enlarged or replaced. Although *Onchopristis* is a batoid and *Pristiophorus* is a shark, the form of attachment of rostral teeth is similar in these forms—more so than between *Onchopristis* and the more closely related *Pristis*.

During a simple dissection to remove a tooth from the rostrum of a sawshark, *Pristiophorus schroederi*, we discovered an incompletely developed tooth lying on its side beneath the skin of the lateral margin of the rostrum. When a further investigation with X-ray revealed more developing teeth (Fig. 3A), tissue sections were made. Our observations led us to examine more closely some of the better ganopristid sawfish material and we found that these fossil forms produced new or replacement teeth in essentially the same way as the modern sawsharks.

For this study we examined the fossil holotypes of the ganopristid sawfishes *Sclerorhynchus solomonis, S. hiram, S. sentus,* and

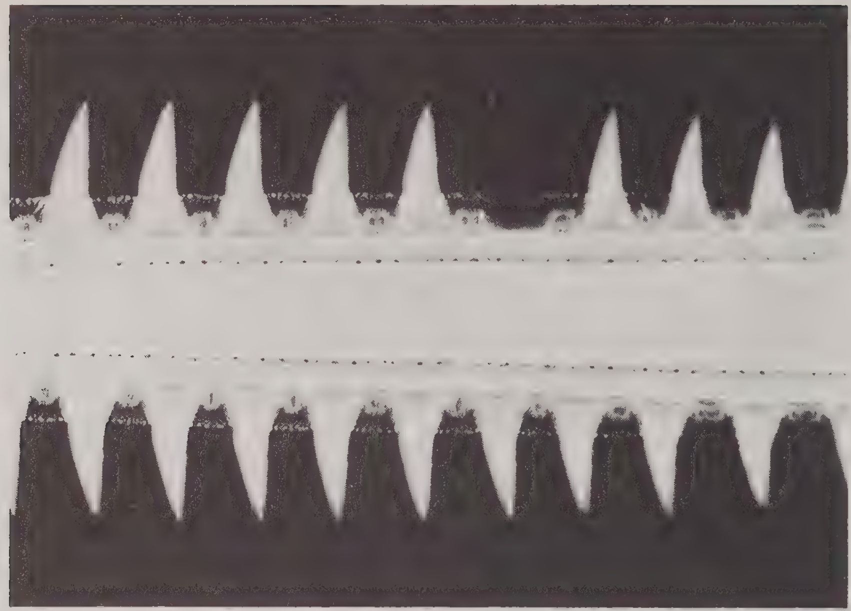

Fig. 1. Radiograph of the middle part of the saw of a young sawfish, *Pristis cuspidatus* (66 cm).

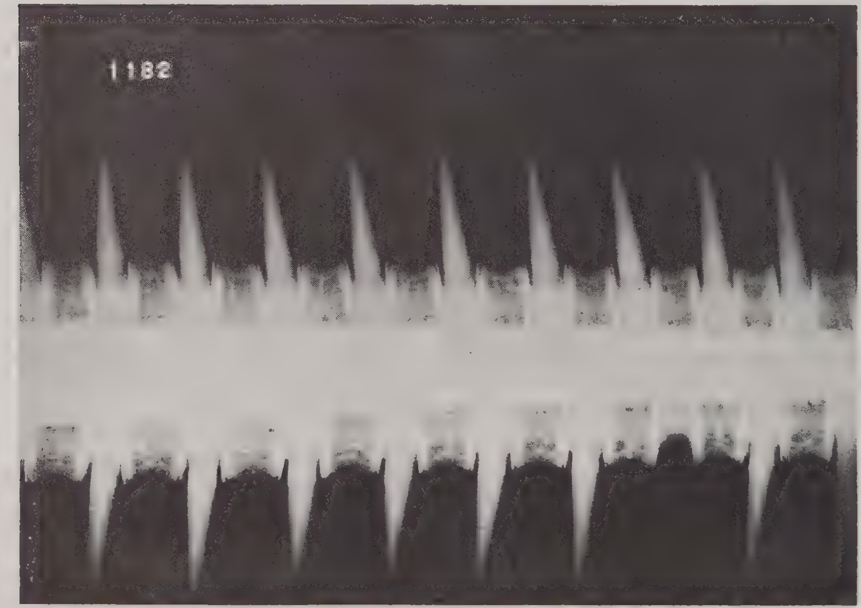

Fig. 2. Radiograph of part of a dried saw from a very large sawfish, *Pristis pectinatus* (estimated total length of sawfish 450 cm).

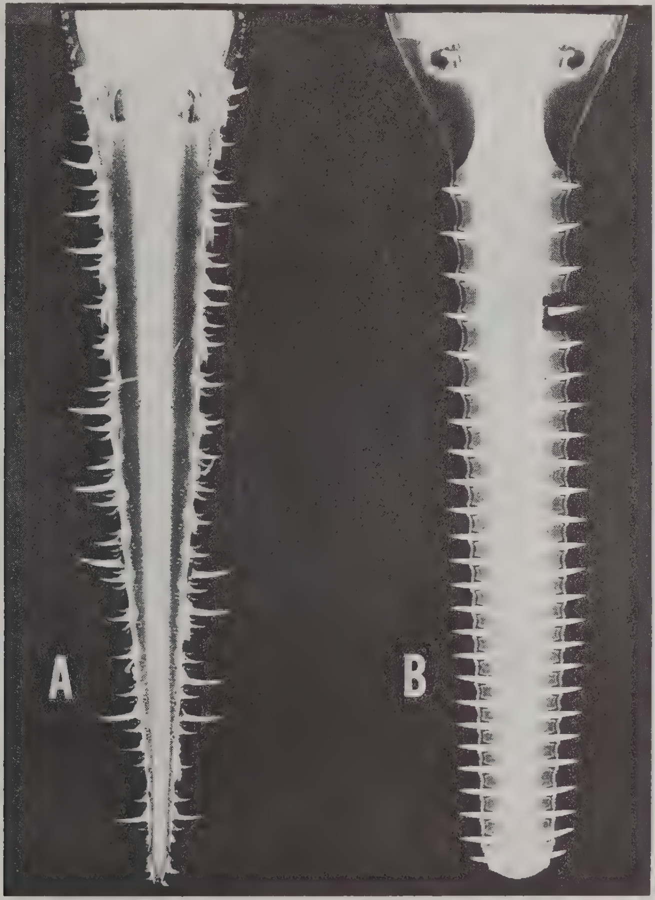

Fig. 3. Radiograph of saws of : A, sawshark, *Pristiophorus schroederi* (81 cm), developing teeth with incompletely formed bases lie under the skin along the margins of the sawshark saw; B, sawfish, *Pristis pectinatus* (78 cm).

the type-species, *S. atavus*, as well as a dozen topotypes of the latter from the late Cretaceous of Lebanon. We reviewed notes on the modern sawsharks, *Pristiophorus* and *Pliotrema*, reported by Springer and Bullis (1960) and examined the following additional material: five specimens of *P. schroederi* from the vicinity of the Bahamas, including a 30 cm newborn female and a 78 cm subadult male; seven specimens of *Pristiophorus japonicus*, 55–66 cm; and one *Pliotrema warreni*, a 135 cm female. Illustrations of the modern sawfish, *Pristis*, were made from material in the U. S. National Museum and the Vanderbilt collection, California Academy of Sciences.

Recent sawfishes, *Pristis*, are large species, some reaching lengths of five m or more; all are confined to tropical and subtropical shore waters. Recent sawsharks, *Pristiophorus* and *Pliotrema*, reach lengths of about 150 cm. Three oriental species of *Pristiophorus* are known from specimens collected from the deeper waters on continental shelves and from upper continental slopes. *P. schroederi*, the only Atlantic species, has been taken from depths of 500–900 m off the Bahamas. *Pliotrema* is restricted to the southeast coast of Africa where it is reported from depths of about 35–450 m.

For our estimates of rostral tooth size patterns we rely chiefly upon our series of *P. schroederi*, which includes a newborn specimen, examples of several intermediate sizes, and a subadult male and subadult female.

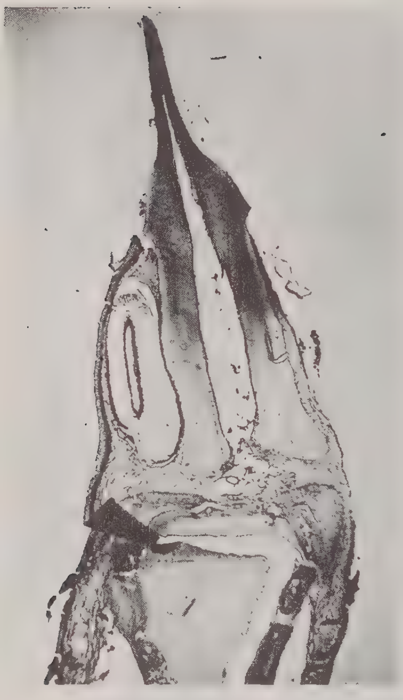

Fig. 4. Longitudinal section of a functional rostral tooth of *Pristiophorus schroederi* with a cross section of a developing tooth (left of functional tooth) beneath the skin.

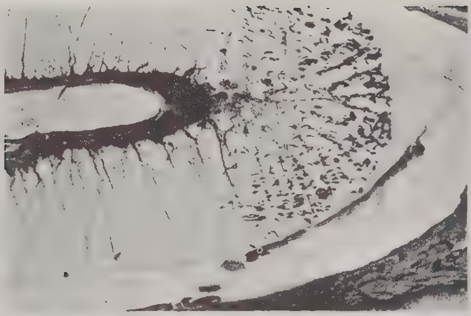

Fig. 5. Cross section of developing *Pristiophorus* rostral tooth showing distribution of pigment in orthodentine.

Rostral Tooth Formation

It is evident that developing rostral teeth in *Pristiophorus* begin with the secretion of an enamel cap. As the enamel crown lengthens, the dentinal wall, which is wholly orthodentine, thickens. Secretion of orthodentine by the odontoblasts does not keep pace with the lengthening of the crown, however, and the pulp cavity of almost completely formed teeth becomes somewhat larger than that of erupted teeth. Developing teeth are softer and more flexible than erupted teeth and often post-mortem compression forms a sulcus on the dorsal or ventral surface in the position of the oversized cavity. After the tooth is fully formed in a recumbent position just beneath the surface of the skin along the lateral margin of the rostrum, the tip swings outward through the skin and forward into the erect position. The base then becomes attached to the rostrum. The edge of the rostrum is flattened and the flat basal end of the tooth merely abuts this edge (Fig. 4). In this respect the tooth attachment in *Pristiophorus* differs from the condition found in many ganopristids where the edge of the rostrum is not flattened and where a basal groove on the tooth forms a saddle-like attachment.

We did not determine what mechanism causes a developing tooth to swing forward and erupt. The action coincides in time with the earliest faint indications of radiographically observable differentiation of the tooth base. Calcification that can be seen on radiographs appears to progress more rapidly along the posterior part of the tooth toward the base than along the anterior part. It seems possible that the formation of orthodentine in the base exerts a gradual upward pressure with the posterior wall of the tooth pushing and the anterior wall pulling the tooth into an erect position. The parts of new teeth that have passed entirely through the skin of the rostrum are already covered by a hard enamel cap and presumably the erect position can be attained only after that portion of the tooth to be exposed is fully developed. We also presume that very little pressure is needed to erect the tooth and to push it through the skin so long as the tooth is capped with very hard material. It is common knowledge that hard surfaced objects may erupt through human skin with only the pressures provided by soft tissues.

Developing teeth in *P. schroederi* (Fig. 5) are pigmented along their anterior edges. Less of this pigment is present in the earlier sets of teeth or single-tooth replacements than in older teeth; consequently, pigmentation aids in the identification of the earlier teeth. The pigment is in the dentine near the boundary between the dentine and the enamel-like coating and is unlike the pigment of teeth of certain mammals, which is incorporated in the enamel itself.

The histology of the rostral teeth of the sawshark *Pristiophorus* is unlike that of most ganopristid sawfishes. Not only is the crown constructed of orthodentine under the enamel cap but the base as well. The orthodentine extends all the way to the base to form the walls of the large basal pulp cavity which opens broadly to the attachment surface. In most ganopristids, at least the base of rostral teeth is constructed of osteodentine. Even in late Cretaceous specimens of *Ischyrhiza*, in which orthodentine extends to the base, a plug of osteodentine usually closes off the pulp cavity from the attachment surface. The one known exception is the fossil sawfish *Sclerorhynchus*, where the rostral teeth have no osteodentine and where the pulp cavity also opens broadly to the attachment surface. The similarity in the rostral tooth histology of *Sclerorhynchus* and *Pristiophorus* led Jaekel (1891) to the conclusion that species referred to *Sclerorhynchus* were actually pristiophorids and not sawfishes. Since then, however, Hay's (1903) description of material from Lebanon demonstrated that strictly batoid characters, such as gills opening on the ventral side and attachment of the pectoral fins to the head are present in *Sclerorhynchus*. Even though we may now recognize no very close relationships between *Sclerorhynchus* and *Pristiophorus*, the two genera do share rostral tooth characters hitherto not found in other elasmobranchs: absence of osteodentine, pulp cavity broadly opening to the attachment surface, and base abutting a flattened edge of the rostrum rather than straddling an obtusely sharp-edged rostrum.

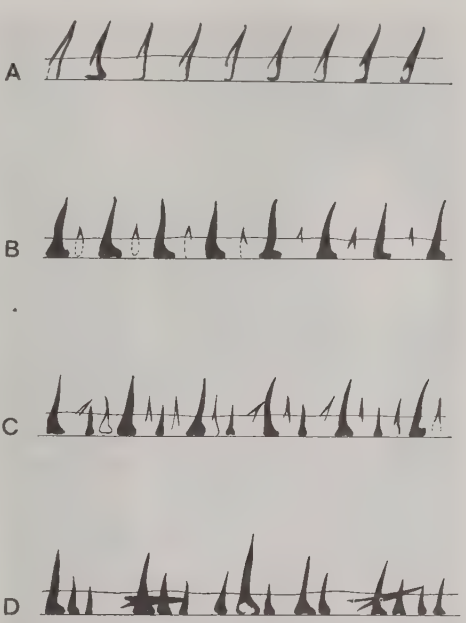

Fig. 6. Diagram of change in rostral tooth arrangement accompanying growth of *Pristiophorus schroederi*. Black indicates extent of calcification in each tooth as shown in radiographs. A, section of saw of newborn 30 cm sawshark shows initial set of teeth with bases not fully calcified; B, saw of 39 cm sawshark, teeth of first set are now fully calcified and second set without calcified bases has erupted; C, saw of 48 cm sawshark, teeth of first and second sets are fully calcified and third set is erupting; D, saw of 81 cm subadult sawshark, a developing tooth shown under skin surface at left, a very large and incompletely calcified tooth in center, and an erupting tooth at right are all replacement teeth filling spaces left by loss of some teeth of first three sets.

Replacement and Addition of Rostral Teeth in *Pristiophorus* and *Pliotrema*

The armament of the head of sawsharks includes: about a dozen comparatively short spines along each margin of the head posterior to the nostrils; two series of enlarged and hooked dermal denticles—one on each side (about 20 hooked denticles in a row in *P. schroederi*) along the ventral surface of the rostrum; and a series of relatively large rostral teeth extending forward from the nostrils and projecting laterally from each margin of the rostrum to form the saw. In the material available to us we see no indications that the numbers of enlarged ventral denticles of the rostrum increase as the sawshark grows or that these spines are replaced if lost. The numbers of lateral rostral teeth increase, however, as the sawshark grows and lost teeth are promptly replaced. In our series of *P. schroederi*, the newborn 30-cm specimen has 23 pairs, the 38 mm type has 46 pairs, and our 80 cm specimen has approximately 80 pairs. The first two specimens appear to have been captured before any tooth losses requiring individual replacement had occurred and the third had an unusually small number of tooth losses and replacements.

Adult and half-grown *Pristiophorus* and *Pliotrema* have lateral rostral teeth of vary-

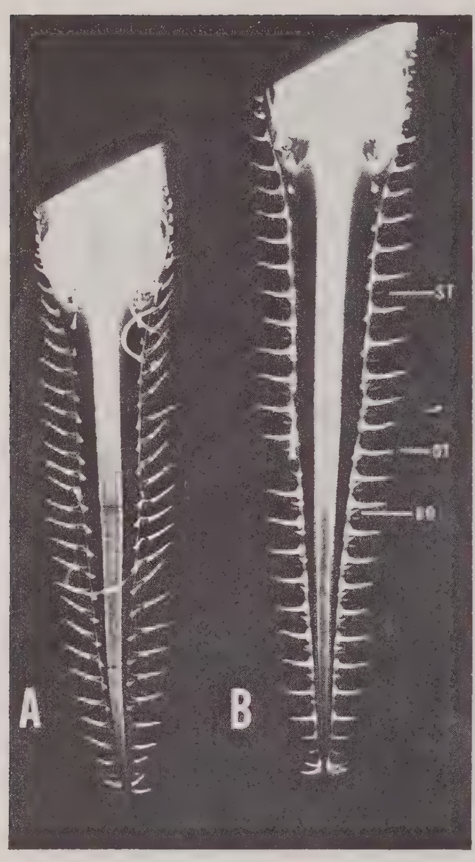

Fig. 7. Radiograph of saws of sawsharks, *Pristiophorus schroederi*. A, saw of newborn 30 cm sawshark with rostral teeth incompletely calcified at their bases and not fully erect; B, saw of 39 cm sawshark, with first set of teeth fully calcified and second set of smaller teeth showing calcification only at their tips. OT, tooth of original set. ST, tooth of second set. DD, enlarged ventral denticle.

ing length; often long, medium, and short teeth are arranged in sequence to form a more or less regular pattern. From the comparatively small number of specimens available we can recapitulate events leading to the development of somewhat variable patterns of rostral tooth length.

At birth, the rostral teeth of *Pristiophorus* are fully developed to their maximum length but are recumbent and are covered by a membrane. The same is true of *Pliotrema* (pers. comm., David Davies, Oceanographic Research Institution, Durban, South Africa). In contrast, the teeth of sawfishes, *Pristis*, are in a fixed, erect position (see Fig. 2) at birth (although covered by a protective sheath during development within the oviducts of the mother) and increase in length after birth (Bigelow and Schroeder, 1953).

Except for a small penultimate pair, the rostral teeth of very young sawsharks are subequal in length; anterior and posterior teeth are only slightly shorter than those of the midpoint of the saw (Fig. 6A and 7A). The rostral teeth of sawsharks do not increase in length after they become fully formed and reach an erect or nearly erect position. After a short period of growth of the shark, a new set of rostral teeth develops and erupts; one new tooth (about one-fourth as long as the original) appears between each adjacent pair (Fig. 6B and 7B). After another period of growth of the shark, a third set of teeth, about one-half to two-thirds as long as the original teeth, develops and erupts—one tooth between each adjacent pair (Fig. 6C).

If no losses occur before the eruption of the third set of rostral teeth, the teeth then occur in a regular sequence: long, intermediate, short, intermediate, long, *etc.* Actually, this pattern begins to break down after the sawshark has acquired the first two sets of teeth, due to accidental loss of teeth and replacement (Fig. 3B). A replacement tooth evidently starts to develop at once whenever a tooth is lost and leaves a space along the margin. New teeth, aside from those of the original set, are roughly proportional in size to the size of the shark at the time of tooth development—whether additional to the functioning set or developed as replacements for lost teeth. The length-sequence pattern becomes progressively less regular, depending upon the extent of tooth losses. Replacement teeth coming in after the sawshark is half grown are as large or larger than teeth of the original set and larger specimens in our series show no evidence of development of small teeth (Fig. 6D).

The new rostral teeth of sawsharks are moderately flexible near the tooth base and from radiographs it can be seen that calcification at their bases is incomplete until the teeth have been in place for an appreciable time. The moderately flexible teeth of very young sawsharks are less likely to be lost, and, although they are very sharp, they may be effective only against small and soft-bodied prey.

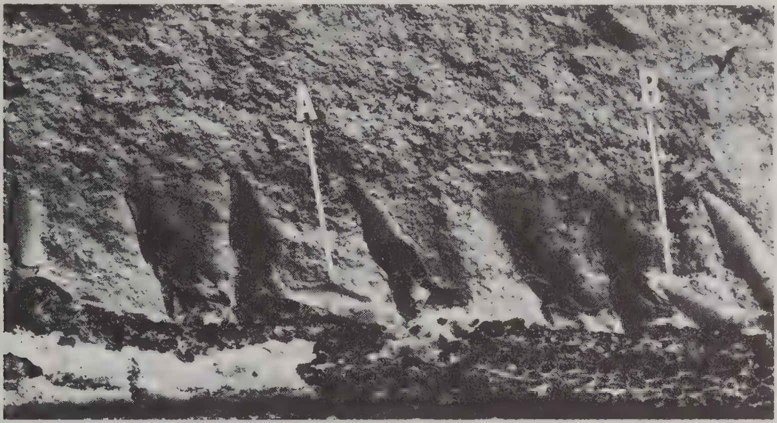

Fig. 8. Developing and functional teeth of the Cretaceous ganopristid, *Sclerorhynchus atavus*. A, least developed tooth without differentiated base. B, erupting tooth with partially differentiated base.

The saws of sawsharks may function as do the saws of sawfishes, *Pristis*, to knock down and immobilize prey. This possibility is suggested by the presence of an unidentified fish 13 cm by 2 cm in the stomach of a 78-cm *P. schroederi*, a fish that appears to be too large for the comparatively feeble jaws to hold in a struggle.

After calcification of rostral tooth bases is complete down to the rims surrounding the pulp cavities, the teeth become rigid but may be easily dislodged. This fact suggests that the saws of sawsharks may be useful structures only for capture of soft-bodied fishes usually found at depths of 400 m or more. Lack of strength in the sawshark's saw may be one reason why sawsharks are normally absent from shallow waters. In contrast, the saws of sawfishes, *Pristis*, are very strong, as they would have to be for effective use against the hard-scaled, firm-fleshed fishes dominating the shallow-water habitats where present-day sawfishes live.

Rostral Tooth Replacement in Ganopristid Sawfishes

Although lost rostral teeth apparently are not replaced in modern sawfishes of the genus *Pristis*, Schaeffer (1963) was led to believe that some kind of tooth replacement must have taken place in the fossil ganopristid, *O. numidus*, by the variation in size of the rostral teeth attached to the calcified rostrum. As described by Stromer (1917), there was no evidence of replacement in this species, but the Stromer specimen was disassociated from the matrix and any teeth not attached to the rostrum would not have been recovered. The *Sclerorhynchus* types and the Lebanon series of this genus that we examined are still in the rock matrix and all have developing teeth and newly formed teeth in the process of erupting. This is particularly well shown in the holotype of *S. atavus* Woodward (1889). Tooth A (Fig. 8) is the least developed, being only about half the length of the other teeth. It lies parallel to the rostrum and has not formed a base (base not differentiated in teeth of *Pristiophorus* at the same stage of development). Also, the dorsal surface has the tell-tale sulcus formed by compression of a tooth with incompletely developed walls and an expanded pulp cavity. Tooth B (Fig. 8) is larger, has a partially developed base, and is in the process of erupting. Both of these teeth, as well as two apparently erupted teeth, have a different preservation from the other entirely erupted teeth in that they are white and opaque, whereas the securely attached teeth are amber-colored and slightly translucent. This difference may reflect a different density of younger teeth.

The rostral teeth of *Pristiophorus* at any one time after a short post-partum period are of several sizes, a result of retention of teeth which erupted at earlier stages in life. Replacements of lost teeth, however, reflect the size of the fish at the time. In the *Sclerorhynchus* specimens we have examined, all of the rostral teeth, in use or just erupting, are the same size. Several interpretations of this can be made. *Sclerorhynchus* may not produce successive sets of teeth of varying size as does *Pristiophorus* despite similarities in rostral tooth development. The rate of accidental rostral tooth loss and replacement may have been greater in *Sclerorhynchus* than it is in *Pristiophorus*. *Sclerorhynchus* may have shed smaller rostral teeth whether or not they were accidentally damaged.

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We thank Stewart Edgell (Department of Geology, American University of Beirut), Colin Patterson (British Museum (Natural History)), and Bobb Schaeffer (American Museum of Natural History) for permission to examine fossil material; and staff members of the U. S. National Museum, University of Michigan Museum of Zoology, Field Museum of Natural History, Stanford University, and California Academy of Sciences, for assistance in making *Pristiophorus* specimens available for study.

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Comparative Embryology of Five Species of Lampreys of the Upper Great Lakes

Allen J. Smith, John H. Howell, and George W. Piavis

The four species of lampreys native to the upper Great Lakes (American brook lamprey, *Lampetra lamotteni*; chestnut lamprey, *Ichthyomyzon castaneus*; northern brook lamprey, *I. fossor*; and silver lamprey, *I. unicuspis*) were collected in various stages of their life cycle and maintained in the laboratory until sexually mature. Secondary sex characters of the four native species are compared. Several batches of eggs of each species were reared at 18.4° C and their development was compared to that of the exotic sea lamprey, *Petromyzon marinus.* The temperature of 18.4° C was previously determined to be optimum for development of the sea lamprey. The high percentage survival of many batches of eggs of native species to prolarvae indicated that 18.4° C was near the optimum for them. Survival to the burrowing stage varied considerably among different batches of eggs from the same species; some batches failed to produce prolarvae. The staging characteristics used for the sea lamprey were applicable to the native species, except for the end point of the burrowing stage. Embryos of the native species in each stage of development appeared according to the time sequence established for the sea lamprey.

Introduction

FIVE species of the family Petromyzonidae are resident in lakes Superior, Michigan, and Huron or their tributary streams (Hubbs and Lagler, 1958): American brook lamprey, *Lampetra lamotteni* (LeSueur); chestnut lamprey, *Ichthyomyzon castaneus* Girard; northern brook lamprey, *I. fossor* Reighard and Cummins; sea lamprey, *Petromyzon marinus* Linnaeus; and silver lamprey, *I. unicuspis* Hubbs and Trautman. The sea lamprey is the only species not indigenous to the upper great Lakes. It first appeared in Lake Huron in the early 1930's and had spread to Lakes Michigan and Superior by 1946 (Applegate, 1950). Chestnut, sea, and silver lampreys are parasitic on fish, often on valuable commercial and sport species.

The sea lamprey has been controlled successfully in Lake Superior by selective toxicants which destroy stream-dwelling larvae (Applegate *et al.*, 1961). These toxicants could be used to control populations of chestnut and silver lampreys since they are also susceptible to sea lamprey larvicides (Howell and Marquette, 1962). Detailed knowledge of the biological characteristics, including its embryology, of a "target species" and its allied species are necessary for the sound development of any control program.

Piavis (1961) described the development of the sea lamprey at various constant temperatures from 7.2° to 26.6° C, and found that 18.4° C was the optimum temperature. He divided the embryological phase of the sea lamprey into 19 stages (Table 1). The objectives of the present studies were: to determine the suitability of 18.4° C as a rearing temperature for the four native species; to determine if Piavis' staging could be used to follow their embryological development; and to compare the time sequence of their development with that of the sea lamprey.

Materials and Methods

The native species of lamprey used in this study were obtained from streams tributary to lakes Huron, Michigan, and Superior. American brook and northern brook lampreys were collected with portable electric shockers. Larvae were obtained from Bear Creek and Platte River, Benzie County, Michigan. Adults were collected on or near their spawning beds in Furnace Creek, Alger County; Laperell Creek, Cheboygan County; Manistee River, Crawford County; and Pendills Creek, Chippewa County, Michigan.

Our major source of chestnut lampreys was from the water-intake screen of the Dow Chemical Co., which is located in Pere Mar-

TABLE 1. STAGE DESIGNATIONS OF LAMPREY EMBRYOS (ADAPTED FROM STAGING CHARACTERISTICS FOR *Petromyzon marinus* GIVEN BY PIAVIS, 1961).

Stage No.	Stage Designation	Initial Point[1]
0	Ovulation	Ovulation of eggs into coelom
1	Zygote	Fertilization
2	2 cells	1st cleavage furrow
3	4 cells	2nd cleavage furrow
4	8 cells	3rd cleavage furrow
5	16 cells	4th cleavage furrow
6	32 cells	More than 16 cells
7	64 cells	More than 32 cells
8	Blastula	More than 64 cells
9	Gastrula	Appearance of blastopore
10	Neural plate and groove	Flattening of dorsal region of embryo from blastopore to anterior extremity
11	Neural rod	Mid-dorsal union of neural folds
12	Head	Raising of anterior portion of embryo above yolk mass
13	Prehatching	Muscular activity in head region (movement)
14	Hatching	Rupture of fertilization membrane
15	Pigmentation	Appearance of melanophores
16	Gill cleft	Appearance of gill slits and velum beat
17	Burrowing prolarvae	Appearance of bilateral eyespots and burrowing ability
18	Larva	Opening of lumen of yolk-filled gut and differentiation of all systems except genital

[1] The end point of each stage is the initial point of the next stage.

quette Lake near the entrance of the Pere Marquette River, Mason County, Michigan. Mature silver lampreys were obtained during their upstream spawning migration on the Waiska River, Chippewa County, Michigan and the Amnicon River, Douglas County, Wisconsin.

Immediately upon arrival in the laboratory lampreys were placed in aquaria, wooden troughs, or large concrete tanks supplied with flowing water from Lake Huron. The holding facility used depended on the life-history stage and degree of sexual maturity of the specimens.

Aquaria were of 57- or 189-liter capacity. The wooden troughs were 0.3 × 0.3 × 3.0 m. Conditions approximating a stream of low velocity were established by inclining each trough approximately 8 cm from the upper to lower end, and covering the bottom with 10–15 cm of gravel. Water introduced at the head flowed over a stopboard at the lower end which maintained a water depth of 5–13 cm. A screen on the stopboard prevented escape. The concrete tanks were of various sizes and the bottoms were covered with 10–15 cm of washed beach sand.

Larval lampreys were placed in the concrete tanks and parasitic-phase individuals were held in aquaria or wooden troughs. Rainbow trout 13–15 cm long were used as food for parasitic lampreys until they matured. Lampreys nearing sexual maturity were held in wooden troughs.

All four species of native lampreys constructed gravel nests in the wooden troughs, and we found that nest building was the most reliable criterion of sexual maturity. Sometimes, however, we used other standards for selecting ripe animals. Applegate (1950) and Vladykov (1949) found that secondary sexual characteristics develop as lampreys approach sexual maturity. The degree of development of these characteristics at full sexual maturity varied among species (Table 2, Figs. 1, 2).

Eggs were fertilized by a procedure similar to that described by Piavis (1961). Eggs and milt were collected in Pyrex or enameled pans 20 × 31 × 5 cm or in glass bowls 10–13 cm diam containing lake water.

Constant-temperature baths maintained the rearing temperature at 18.4° C. Pyrex or enameled pans used for incubation, were

TABLE 2. SECONDARY SEXUAL CHARACTERISTICS OF THE FOUR SPECIES OF NATIVE LAMPREYS AT THE TIME OF SEXUAL MATURITY.

	♂♂			♀♀	
Species	Mid-dorsal Ridge	Urogenital Papilla	Cloacal Area[1]	Post-anal Keel	Body Size[2]
Lampetra lamotteni	Slightly developed or lacking	Protruded through cloaca; extends beyond ventral margin of body	Swollen and inflamed	Prominent; convoluted slightly; crescentic from lateral aspect	Distended from post-cardial region to the cloaca; dorsal flexure beginning at cloaca and continuing posteriorward; ova visible through body wall
Ichthyomyzon fossor	Slightly developed or lacking	Protruded through cloaca; extends beyond ventral margin of body	Swollen and inflamed	Prominent; convoluted slightly; elongate extending from cloaca to caudal peduncle	Distended from post-cardial region to the cloaca; dorsal flexure beginning at cloaca and continuing posteriorward; ova visible through body wall
Ichthyomyzon castaneus	Slightly developed or lacking	May or may not be protruded through cloaca; when protracted extends beyond ventral margin of body	No swelling or inflammation at sexual maturity	Prominent; normally not convoluted; crescentic from lateral aspect	Greatly distended from post-cardial region to the cloaca; little or no dorsal flexure; ova not visible through body wall
Ichthyomyzon unicuspis	Always present; not always prominent	May or may not be protruded through cloaca; when protracted extends beyond ventral margin of body	No swelling or inflammation at sexual maturity	Prominent; normally not convoluted; elongate extending from cloaca to caudal peduncle	Greatly distended from post-cardial region to the cloaca; little or no dorsal flexure; ova not visible through body wall

[1] The males of all species are characteristically flattened mid-ventrally posterior to the cloaca. [2] Body size refers to distension of the coelomic cavity.

submersed in the constant temperature bath and aerated by stone air-breakers; only one batch of eggs was placed in each bath to eliminate the possibility of accidental interchange of embryos among the submersed pans.

When glass bowls were used for hatching, each was submersed in 5–6 liters of water in 10-liter (25 cm deep) Pyrex battery jars placed in the constant temperature bath, in which water was 13 cm deep. Several battery jars could be placed in each bath since embryos could not be exchanged accidently between jars. Each jar was aerated and the flow was adjusted to avoid excessive movement of eggs.

For the sea lamprey Piavis (1961) took the first staging samples 20–30 min after fertilization, and thereafter samples were removed at the following hr: 1, 2, 3, . . . 12, 14, 16, 18, 20, 24, 28, 32, 40, 48, . . . 72. After the 72nd hr, samples were taken at 12-hr intervals. When experiments lasted longer than 18 days samples were taken each 24 hr.

Our sampling schedule and staging sequences for the native species were based on hourly samples through the 24th hr and a minimum of two samples each 24 hr thereafter. The times of the later samplings were governed by the anticipated time of appearance of various stages. We do not feel that this variation in sampling biased comparisons of the time sequences of development of the sea lamprey and the native species.

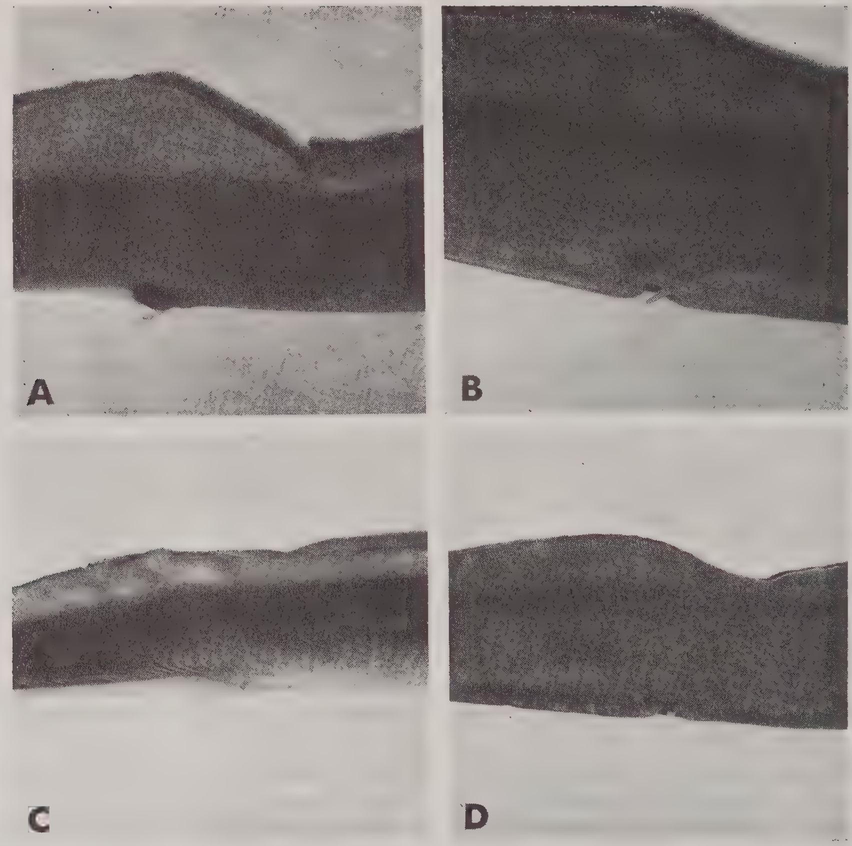

Fig. 1. Urogenital papilla and condition of cloacal area at full sexual maturity in males of four species of lampreys. A, American brook lamprey, *Lampetra lamotteni*; B, chestnut lamprey, *Ichthyomyzon castaneus*; C, northern brook lamprey, *I. fossor*; and D, silver lamprey, *I. unicuspis*.

SUITABILITY OF 18.4° C AS A REARING TEMPERATURE

Piavis (1961) incubated sea lamprey eggs at ten constant temperatures that ranged from 7.2° to 26.6° C. Sea lamprey eggs were extremely sensitive to temperature; burrowing prolarvae (stage 17) were produced only within the relatively narrow range of 15.5°–21.1° C. A constant temperature of 18.4° C was considered optimum since survival was 78% compared to 12% at 15.5° C and 5% at 21.1° C.

Similar experiments were not made for the native lampreys; we used 18.4° C as a rearing temperature because we wanted to compare the development of the native species with that of the sea lamprey. We assumed that the optimum temperature for the development of sea lampreys would be suitable for the native lampreys since all five species spawn in streams of the same physical characteristics and often share the same larval habitat.

Success in the production of stage 17 prolarvae from eggs of the native lampreys incubated at 18.4° C varied considerably (Table 3). All batches of chestnut and northern brook lampreys, five of 13 batches of American brook lampreys, and four of seven batches of silver lampreys produced prolarvae. The suitability of 18.4° C for rearing native species was shown by the high percentage survival in one or more batches for each species.

Because the rearing temperature was constant, it could not have been responsible for the failure of some batches to produce prolarvae and the variability in production among others. It is possible that viability

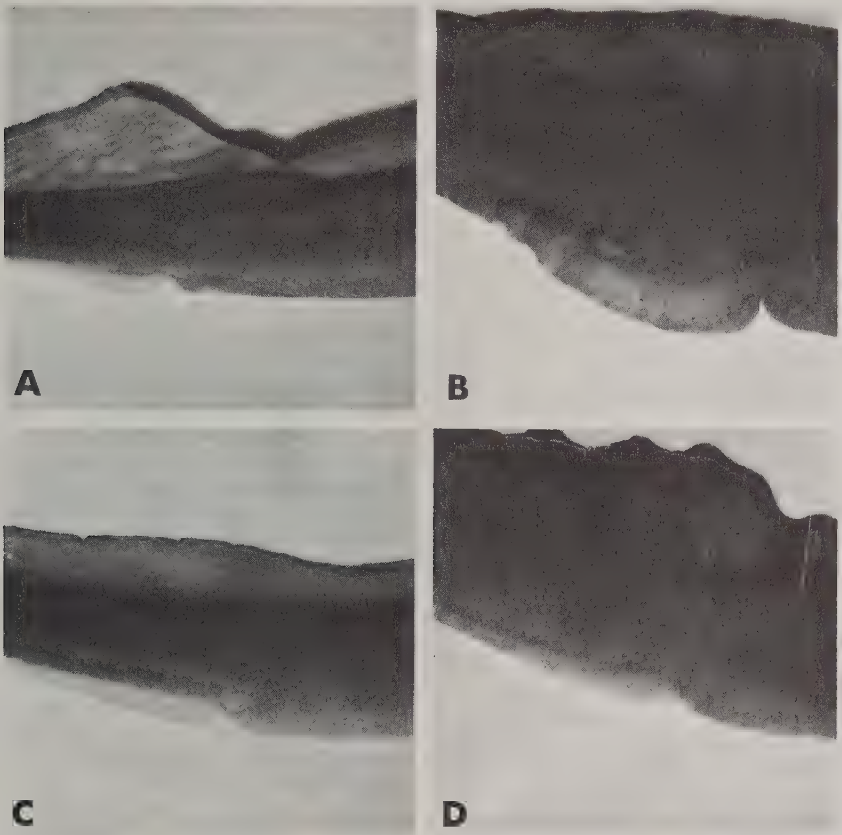

Fig. 2. Post-anal keel at full sexual maturity in females of four species of lampreys. A, American brook lamprey, *Lampetra lamotteni*; B, chestnut lamprey, *Ichthyomyzon castaneus*; C, northern brook lamprey, *I. fossor*; and D, silver lamprey, *I. unicuspis*.

naturally varies among eggs of lampreys. Although Piavis (1961) found 78% production from a single batch of sea lamprey eggs reared at 18.4° C, we have found that the yield varies considerably among batches of sea lamprey eggs incubated at this temperature. The variability was similar to that in the present study of native species—high to low production and sometimes complete failure.

Comparative Embryological Staging

The stages of the sea lamprey described by Piavis (1961) are based on morphological "end points" and on activity and movement. We were also able to follow the embryonic development of the native species with these same characteristics. The beginning and end point of each stage can be distinguished easily except the end point for stage 17. An important characteristic of this stage in the sea lamprey is the posterior progression of transparency as the gut differentiates. The opening of the digestive system from the mouth to the anus is the end point. In the native species, the wall of the gut retained a coating of yolk that made it difficult to determine when the lumen of the gut opened.

The native species exhibited minor differences in development from the sea lamprey in stages 11, 12, and 13, but these differences were so slight that they did not prevent the use of criteria for the sea lamprey to identify these stages of the native forms. The principal difference was the relation between the developing embryo and the yolk (Figs. 3, 4). During the later phase of stage 11 in the sea lamprey, the embryo extended two-thirds of the way around the yolk

Table 3. Highest Developmental Stage Attained for Each Batch of Eggs from Native Lampreys Reared at 18.4° C and Percentage Survival to Burrowing Prolarvae (Stage 17).

Species and Highest Stage Attained	Production Stage 17 Prolarvae (Percentage)	No.[1] of Eggs
Lampetra lamotteni		
2	0.0	354
10	0.0	480
11	0.0	3417
12	0.0	1565
12	0.0	2799
13	0.0	3292
14	0.0	1073
16	0.0	934
17	0.3	1049
17	57.3	532
17	94.6	1314
17	95.5	1593
17	96.1	1446
Ichthyomyzon castaneus		
17	16.3	1333
17	47.7	1910
17	58.7	2683
17	80.9	4186
I. fossor		
17	0.4	3121
17	17.4	898
17	35.0	1066
17	62.0	703
17	84.3	2336
17	90.8	986
17	91.4	1703
17	93.2	1161
17	94.7	472
I. unicuspis		
8	0.0	4390
9	0.0	5167
14	0.0	5202
17	54.2	1636
17	65.6	4346
17	80.1	1580
17	82.9	1782

[1] These numbers are not representative of the fecundity of these species. Sometimes eggs from more than one female were combined. Also, eggs from a single female were split into more than one experimental batch.

mass, but in the native species it extended over only one-half of the yolk mass.

For all species, termination of stage 11 and initiation of stage 12 were characterized by the elevation of the head from the yolk mass. The head in the sea lamprey was elevated from a ventral point but the head in the native species was elevated more dorsally. Consequently, the head in the embryos of native lampreys generally had a more anterior orientation than the anterioventral orientation in the sea lampreys. Since embryos extended along a lesser curvature of the yolk mass in native lampreys than in sea lampreys, a greater length of the native lamprey embryos was elevated and a longer, anteriorly oriented "neck" region resulted.

In the late phase of stage 12, the head and "neck" region curves or bends toward the posterioventral portion of the embryo in sea lampreys but is nearly straight and anterior in the native lampreys. The difference in orientation created a much larger perivitelline space in the native lamprey embryos, than in sea lamprey embryos. Termination of stage 12 in all embryos was identical—muscular activity that was evident from movement of the head and "neck" within the fertilization membranes.

Comparative Timing of Embryological Stages

Piavis (1961) based the time intervals for each developmental stage of the sea lamprey on the first and last appearance of each stage. The time sequence of embryological development in the native lampreys was obtained by combining the observational data from all batches of each species. The earliest and latest observation of each developmental stage in the native lamprey embryos are given with similar data for the sea lamprey in Fig. 5.

The initial appearance of stages in the native species was generally earlier than in the sea lamprey in stages 2 through 8. Following stage 8, embryos of the American brook lamprey appeared to be earliest of all species for eight of nine stages. Onset of stages in embryos of the chestnut and northern brook lampreys after stage 8 was either early or coincided with corresponding stages in the sea lamprey. The initial appearance of post-blastular stages in the silver lamprey was early at stages 13, 15, 16, and 17; late at stages 11, 12, and 14; and coincided with the sea lamprey at stages 9 and 10.

The latest observation time of various developmental stages in the native species differed considerably from that of the sea lamprey through stage 7. Generally, these end points occurred later for native lampreys,

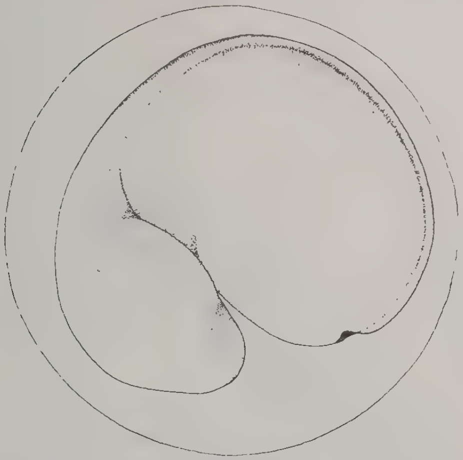

Fig. 3. Line drawing of developing embryo of *Petromyzon marinus* in stage 11. The embryo extends around three-fourths of the yolk mass.

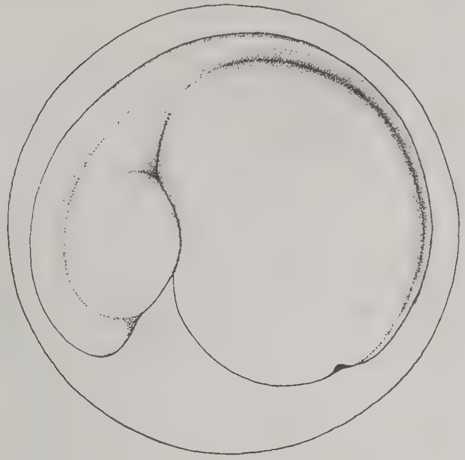

Fig. 4. Line drawing of developing embryo of *Ichthyomyzon unicuspis* in stage 11. The embryo extends around approximately one-half of the yolk mass as is typical with all the native species.

except for stage 6, where no embryos of the native species were found at the time of the end point of that stage for the sea lamprey. In stages 8–16 end points for embryos of the chestnut, northern brook, and silver lampreys were later than those for the sea lamprey. American brook lamprey embryos usually were later than the sea lamprey except stages 9 and 16.

In the determination of the time sequence of the development of lamprey eggs by subsampling large numbers, the possibility exists that the subsample may not contain all the stages of development represented in the entire batch. This problem exists when the subsamples are used to determine the earliest and latest time of developmental stages since only a few embryos at these points of development may be present. The situation is illustrated by the data for earliest appearance of stages 4 and 5 in the northern brook and stages 12 through 15 in the silver lamprey. For example, the earliest appearances of stages 4 and 5 in the northern brook lamprey was 5 hr for both stages. It is obvious, however, that stage 4 (eight cells) occurs earlier than stage 5 (16 cells). It must also be remembered that we pooled data from a number of batches and the observations are not always from the same batch.

The combination of data for all batches of each native species, both "good" and "bad," may have introduced some bias into our comparison with the sea lamprey, since Piavis (1961) based his timing on a single "healthy" or "normal" batch of eggs. As mentioned previously in the discussion of the suitability of 18.4° C as a rearing temperature, some batches did not produce stage 17 prolarvae. We were unable to anticipate which batches would fail and therefore maintained staging records as long as live embryos could be found. In no instance did we include abnormal embryos in the staging data.

The duration of embryological stages is usually considered as the time interval between the first appearance of a stage and the earliest appearance of the following stage. This interval can be determined accurately if the development of individual eggs is followed. In subsampling large groups of embryos, however, development of individual eggs can not be followed. Instead, duration was interpreted both as the length of time eggs were found in a particular stage of development and as the interval between the first appearance of a stage and initial observation of the next developmental stage. The former provides an approximation of the maximum duration of a developmental stage and the latter gives a possible minimum (Table 4).

The duration as estimated from first appearance of successive stages does not vary greatly among the four native species and

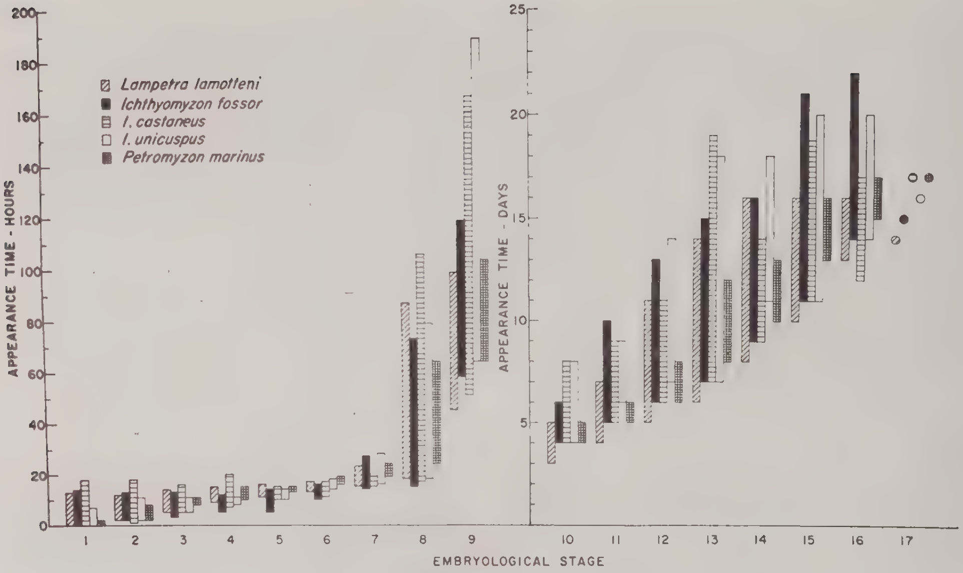

Fig. 5. Duration of embryological stages in five species of lampreys.

the sea lamprey; the maximum length of time most stages could be found in the native species is much longer. The longer duration may have been influenced by dead or dying embryos in the staging data or by differences among batches.

Criteria used to separate live from dead embryos were the same as those used by Piavis (1961). These characteristics develop rapidly during the cellular stages—particularly the formation of vacuoles in the heavily yolk-laden cells of the vegetal hemisphere. Following gastrulation the exact point at which an embryo is dead becomes progressively more difficult to determine. The best indication of death is sloughing of cells from the embryo into the perivitelline space and clouding of the fertilization membrane.

TABLE 4. DURATION (HR, STAGES 1–9; DAYS, STAGES 10–16) OF EMBRYOLOGICAL STAGES OF FIVE SPECIES OF LAMPREYS. (Data for *Petromyzon marinus* from Piavis, 1961.)

	Lampetra lamotteni		*Ichthyomyzon castaneus*		*I. fossor*		*I. unicuspis*		*P. marinus*	
Stage	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
1	13	2	18	1	14	2	7	2	2	2
2	10	3	17	4	11	1	9	3	6	6
3	9	4	11	2	10	2	6	3	3	2
4	6	2	13	3	7	0	3	2	5	3
5	5	2	5	1	9	5	4	4	3	3
6	4	2	6	4	6	4	4	2	3	3
7	8	3	4	2	13	1	12	2	5	5
8	69	27	89	39	58	43	61	46	40	40
9	54	27	116	45	61	38	125	32	40	32
10	2	1	4	1	2	1	4	2	1	1
11	3	1	4	1	5	1	3	1	1	1
12	6	1	5	1	7	1	7	0	2	2
13	8	2	12	2	8	2	11	4	4	2
14	8	2	5	2	7	2	7	0	3	3
15	6	3	8	1	10	3	9	3	3	2
16	3	1	5	5	8	1	6	2	2	2

These characteristics undoubtedly develop at an undetermined time after death. Since death is so difficult to determine in post-blastular stages, some of the observations of the presence of these stages could have been based on dead or dying embryos. Some abnormalities often occur before death, however, such as enlarged blastopores, pigmentation before "hatching," unusually curved trunk regions, enlarged and transparent pericardia, and balloon mouths caused by failure of the stomadaeum to open. Thus, exclusion of abnormal embryos from staging should have eliminated many of the dying embryos.

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BUREAU OF COMMERCIAL FISHERIES HAMMOND BAY BIOLOGICAL STATION, MILLERSBURG, MICHIGAN 49759 AND DEPARTMENT OF ANATOMY, SCHOOL OF DENTISTRY, UNIVERSITY OF MARYLAND, BALTIMORE, MARYLAND 21201.

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LAMPREY CONTROL AND RESEARCH IN THE UNITED STATES

Bernard R. Smith

APPENDIX C

LAMPREY CONTROL AND RESEARCH IN THE UNITED STATES

Bernard R. Smith

Bureau of Commercial Fisheries
U. S. Fish and Wildlife Service

Severe budget restrictions curtailed several phases of the sea lamprey program in 1967. All chemical control on tributaries of Lake Huron was discontinued on July 1 and several field research projects were reduced or terminated. The number of spawning-run sea lampreys taken at barriers on United States streams of Lake Superior again declined. The final count from the 16 barriers was 30 percent below the catch in 1966 and only 5 percent of the record catch of 1961. This year was the first since barriers have been operated that at least one weir did not capture more than 1,000 sea lampreys. Progress of chemical control on Lakes Superior and Michigan was excellent. Twenty-nine streams were treated in the 2 lakes and 14 Lake Huron tributaries were treated in the first half of the year (Table 1).

Lake Superior surveys

Forty-six previously treated streams were surveyed in 1967 and sea lamprey ammocetes were found in 27. Larvae in 15 streams were of size and number to require treatment;

Table 1. Summary of chemical treatments in United States waters of the Great Lakes in 1967.

	Number of streams	Discharge at mouth (cfs)	Stream miles treated	Lampricide used (pounds)	Synergist used (pounds)
Superior	17	2,628	304	27,672	755
Michigan	12	1,399	414	31,124	67
Huron	14	456	189	11,436	44
Total	43	4,483	907	70,232	866

13 were treated and 2 are scheduled for treatment in 1968. Re-surveys of 32 "negative" streams, including 10 on Isle Royale, showed no change of status.

Bayer 73 granules were used to survey deep or turbid sections of 8 streams where the use of electric shockers was impractical. A total of 46,250 square feet was treated with 333 pounds of granules. Sea lamprey ammocetes were recovered in 1 stream, native lamprey ammocetes in 4, and no ammocetes in 3. The St. Louis River and its tributaries below the barrier dam at Fond du Lac were surveyed with electric shockers and granular Bayer 73. No lampreys were found. Surveys were generally efficient in the tributaries, but deep water, heavy stream vegetation, and poor weather limited the effectiveness of the granules and hindered observations in the main stream.

Sea lamprey nests were found in 14 of the 19 Lake Superior streams examined for spawning adult sea lampreys in 1967. Fifty-one nests were counted in the index areas on the Bad River. Previous nest counts in the Bad River were 38 in 1966, 44 in 1965, and 189 in 1964. Spawning in Minnesota tributaries appeared heavier; 23 nests were found in 5 streams whereas only 13 nests were found last year. Most spawning surveys were hindered by high or turbid waters, and runs of adults may have been larger than indicated.

Lake Superior chemical treatments

Seventeen streams of Lake Superior having a total discharge of 2,628 cfs were treated (Table 2). Of these, 14 were treated with TFM and 3 with a synergistic mixture containing 99 percent by weight of TFM and 1 percent 5,2'-dichloro-4'-nitrosalicylanilide (TFM-1B). Two streams were treated for the second time, 11 for the third time, 2 for the fourth time, and 2 for the sixth time. The latter are treated often to control ammocete populations in lakes within their systems. Few residual ammocetes from previous treatment were in collections from the treated streams. Moderate numbers of re-established ammocetes were found in all streams except the Cranberry River, Seven Mile Creek, and Laughing Whitefish River, where re-established populations were small.

The Big Garlic River, one of the streams treated for the sixth time, was treated with granular Bayer 73 on its Sauxhead Lake delta. The effectiveness of the granules is indicated by collections from the 1966 and 1967 treatments. In 1966, 481 sea lamprey ammocetes were collected compared with 15 from

Table 2. Details on the application of lampricide to tributaries of Lake Superior in 1967.

Stream	Date	Discharge at mouth (cfs)	Concentration (ppm)		Lampricide (pounds)	Synergist (pounds)
			Minimum effective	Maximum allowable		
Fish Creek (Eileen)	April 28	85	3.0	9.0	990	. . .
Amnicon River	May 1	125	1.0	2.5	918	. . .
Nemadji River	May 13	408	3.0	5.0	3,492	. . .
Laughing Whitefish River	May 18	43	2.0	5.0	432	. . .
Little Garlic River	May 23	19	1.5	3.5	108	. . .
Big Garlic River	July 7	25	2.0	4.0	180	202[1]
Iron River	July 12	87	1.0	3.5	594	8
Beaver Lake Outlet	July 18	5	3.0	7.5	54	75[1]
Seven Mile Creek	July 19	17	3.0	8.0	144	. . .
Sucker River	July 27	80	1.5	5.0	684	75[1]
Ontonagon River	Aug. 16	820	3.0	6.0	10,332	. . .
Salmon-Trout River	Aug. 21	34	4.0	7.0	234	100[1]
Rock River	Aug. 31	20	6.0	10.0	375	. . .
Sturgeon River	Sept. 13	180	4.0	10.0	1,605	. . .
East Sleeping River	Oct. 3	8	3.0	9.0	570	200[1]
Cranberry River	Oct. 10	32	3.5	8.0	465	. . .
Tahquamenon River	Oct. 18	640	3.0	5.0	6,495	95
Total	. . .	2,628	. . .	. . .	27,672	755

[1] Heavy granules of 5 percent Bayer 73.

a similar treatment this year. In addition to regular treatment, granular Bayer 73 was applied to the deltas of Little Beaver Creek in Little Beaver Lake and Sucker River in East Bay. Sea lamprey ammocetes surviving the previous treatment were collected on both deltas. Treatment will be repeated in 1968.

In summary, 168 treatments have been completed since 1958 on 75 streams; 19 streams have been treated once, 29 twice, 21 three times, 4 four times, and 2 six times. Sea lamprey ammocetes found in 4 other streams disappeared before treatment was necessary.

Lake Superior electric barrier operations

Electric barriers were operated in 1967 on 16 streams tributary to the south shore of Lake Superior from early April to July 13. A cold spring slowed the migration and unprecedented floods in mid-June inundated several weir sites, allowing some escapement.

The number of spawning migrants declined again in 1967. The total of 3,362 adults taken was 1,399 less than in 1966 and 63,339 less than the record high in 1961 (Table 3). The run developed slowly. Only 13 percent of the run was taken through May 25 compared with 31 percent in 1966. The peak was

Table 3. Catches of adult sea lampreys for comparable periods from 16 Lake Superior streams, 1961-1967.

Stream	1961	1962	1963	1964	1965	1966	1967
Betsy River	1,366	316	444	272	187	65	57
Two Hearted R.	7,498	1,757	2,447	1,425	1,265	878	796
Sucker River	3,209	474	698	386	532	223	166
Miners River	220	64	107	74	23	85	75
Furnace Creek	1,012	132	142	93	199	118	119
Rock River	3,660	399	353	229	237	158	439
Chocolay River	4,201	423	358	445	563	260	65
Iron River	2,430	1,161	110	178	283	491	643
Huron River	4,825	70	201	363	637	8	2
Silver River	5,052	267	760	593	847	1,010	339
Sturgeon River	427	397	1,445	375	135	259	43
Misery River	962	80	24	12	3	10	26
Firesteel River	1,118	70	178	327	11	15	9
Brule River	22,478	2,026	3,418	6,718	6,163	226	364
Middle River	3,502	311	48	45	52	17	19
Amnicon River	4,741	879	131	232	700	938	200
Total	66,701	8,826	10,864	11,767	11,837	4,761	3,362
Percentage change		-86.8	+23.1	+8.4	+0.6	-59.8	-29.4

between May 26 and June 4, when 25 percent of the total catch was taken. The migration then stabilized for 30 days and declined slowly during the last 10 days of weir operation.

The number of sea lampreys captured in weirs east of the Keweenaw Peninsula declined 22.8 percent and the number in western streams declined 48.8 percent from 1966. The counts from the Silver and Amnicon Rivers, the major producers in 1966, declined 66 and 79 percent, respectively. (The weir in the Ocqueoc River, Lake Huron, captured 674 adult sea lampreys compared with 3,272 in 1966.)

The average length and weight of mature sea lampreys from barriers in 10 index streams of Lake Superior increased in 1967. The average length was 16.5 inches in 1967 compared with 16.0 inches in 1966. The weight increased from 5.2 ounces in 1966 to 5.9 ounces in 1967. The percentage of males among adult sea lampreys captured at Lake Superior weirs continued to decline. Males composed 32.7 percent of the sample compared with 41.2 percent males in 1966 and 69.6 percent in 1962 when males reached the peak of dominance. The ratio of males to females is the lowest recorded from Lake Superior streams.

The number of longnose suckers in 9 tributaries to Lake Superior declined in 1967, whereas the numbers of white suckers and rainbow trout increased slightly. Sea lamprey scars on large rainbow trout from selected streams declined to 1.4 percent (Table 4), giving further evidence of the success of sea lamprey control.

Lake Michigan surveys

Seventeen Lake Michigan tributaries were surveyed in preparation for scheduled chemical treatments. Eight of the streams were treated and 9 are scheduled for treatment in 1968. An additional 31 tributaries treated previously were examined to determine the size and distribution of re-established larval populations. Sea lamprey larvae were found in 24. Initial surveys of 4 Beaver Island streams and 1 on Garden Island yielded no ammocetes. The drainages are inconsequential and provide little potential for production of lampreys. Re-surveys of 35 previously "negative" streams discovered one ammocete in each of 2 streams, the Big Suamico and the Kewaunee Rivers in Wisconsin.

Population estimates were made on sea lamprey ammocetes in Springer Creek, Menominee County, Michigan, from survey and chemical treatment collections. *Ichthyomyzon* spp. larvae

Table 4. Percentage of sea lamprey scarring on rainbow trout[1] from tributary streams of Lake Superior, 1960-1967.

[The figures in parentheses indicate the number of rainbow trout examined.]

Stream	1960	1961	1962	1963	1964	1965	1966	1967
Two Hearted River	24.0 (208)	2.8 (178)	4.6 (217)	1.6 (256)	1.6 (62)	1.4 (279)	0.4 (242)	1.2 (496)
Sucker River	9.7 (175)	2.4 (166)	4.2 (257)	5.6 (179)	3.0 (231)	1.3 (312)	1.4 (290)	1.9 (158)
Miners River	22.9 (83)	18.0 (100)	3.5 (201)	3.3 (90)	5.2 (77)	5.8 (120)	3.0 (164)	1.3 (224)
Furnace Creek	16.0 (25)	13.6 (22)	0.0 (8)	25.0 (4)	12.5 (8)	0.0 (13)	0.0 (14)	2.6 (38)
Huron River	12.2 (245)	11.5 (233)	2.3 (398)	3.4 (291)	2.2 (180)	5.6 (270)	3.8 (421)	2.3 (399)
Silver River	0.0 (21)	4.2 (72)	2.8 (71)	1.8 (56)	9.1 (55)	4.0 (50)	0.0 (42)	6.3 (16)
Misery River	2.3 (43)	3.2 (31)	0.0 (9)	0.0 (13)	0.0 (5)	. . . (0)	0.0 (11)	0.0 (9)
Firesteel River	0.0 (45)	0.0 (114)	0.0 (43)	0.0 (47)	0.0 (18)	0.0 (29)	0.0 (29)	0.0 (17)
Brule River	7.6 (92)	1.2 (82)	2.1 (140)	0.9 (227)	3.4 (177)	4.3 (255)	0.9 (414)	0.0 (271)
All streams	13.6 (937)	6.2 (998)	3.1 (1,344)	2.7 (1,163)	3.4 (813)	3.2 (1,328)	1.8 (1,627)	1.4 (1,628)

[1] Over 12 inches, total length.

(exotic to Springer Creek) were distributed as marked animals. Estimates of sea lamprey abundance were 1,226 from survey collections and 1,995 on the basis of after treatment collections. These estimates are part of a continuing project to establish a means of assessing abundance of lampreys in Great Lakes tributaries.

Lake Michigan chemical treatments

Chemical treatments began in April and continued until late October. Stream water discharges generally were higher than for the first treatments and more TFM was required.

Twelve streams having a combined discharge of 1,399 cfs were treated (Table 5). Three streams scheduled for 1967 were not treated. Crystal River and Acme Creek contained no sea lamprey larvae and the Boardman River contained ammocetes too small to require immediate treatment. The Betsie River, Benzie County, and the Ford River, Delta County, were treated with a synergistic mixture containing 99.5 percent by weight of TFM and 0.5-percent 5,2'-dichloro-4'-nitrosalicylanilide which gave an estimated savings of 6,900 pounds of TFM. Re-established sea lamprey larvae were more numerous in the Betsie, Little Manistee, and Platte Rivers than at the time of first treatment. The numbers of ammocetes in the other streams varied little from the numbers during previous treatments.

Mortality of fish was slight on all treated streams except in the Platte River. Some large spent rainbow trout were killed in an area of stream where the trout, hand-stripped of eggs, had been released by Platte River Hatchery personnel before treatment. Mortality of brown trout experienced during first treatment of the Platte and Little Manistee Rivers was avoided by treating in April and July, respectively, rather than in September.

Bureau personnel from the Hammond Bay and Ludington Stations assisted the Fish Division of the Michigan Department of Conservation in a fish eradication experiment on the Muskegon River between Big Rapids and Rogers Dam.

Lake Huron surveys

Pretreatment surveys were completed on 8 Lake Huron tributaries. Posttreatment surveys were made on 19 streams. Re-established sea lamprey ammocetes and a few residual ammocetes were found in 5 of the streams. Nine others had re-established populations. Sea lamprey larvae were absent in the 5 streams. Thirty-four "negative" streams were resurveyed. Sea lamprey larvae were found for the first time in Martineau Creek in Mackinac County, Michigan. The other 33 streams remained negative.

Lake Huron chemical treatments

Fourteen tributaries, having a total discharge of 456 cfs, were treated between May 11 and June 29 (Table 6). Eleven streams were treated for the first time and 3 streams for the second time. Treatment costs were high because of high water and several streams that contain sections that required separate

Table 5. Details on the application of lampricide to tributaries of Lake Michigan in 1967.

Stream	Date	Discharge at mouth (cfs)	Concentration (ppm)		Lampricide (pounds)	Synergist (pounds)
			Minimum effective	Maximum allowable		
Platte River	April 19	422	5.0	12.0	8,760	. . .
Good Harbor Creek	April 26	69	4.0	10.0	792	. . .
Mitchell Creek	April 27	16	6.0	14.0	466	. . .
Springer Creek	June 3	6	6.0	12.0	90	. . .
Ford River	June 5	430	4.0	10.0	10,980	53
Little Manistee River	July 19	220	5.0	12.0	6,642	. . .
McGeach Creek	July 31	2	11.0	25.0	136	. . .
Betsie River	Aug. 30	200	3.0	6.0	2,448	14
Hog Island Creek	Oct. 26	4	5.0	10.0	180	. . .
Squaw Creek	Oct. 28	8	3.5	8.0	216	. . .
Valentine Creek	Oct. 29	15	2.0	4.0	306	. . .
Deadhorse Creek	Oct. 30	7	4.0	10.0	108	. . .
Total	. . .	1,399	. . .	. . .	31,124	67

Table 6. Details on the application of lampricide to tributaries of Lake Huron in 1967.

Stream	Date	Discharge at mouth (cfs)	Concentration (ppm) Minimum effective	Concentration (ppm) Maximum allowable	Lampricide (pounds)	Synergist (pounds)
Schmidt Creek	May 11	52	3.0	10.0	769	. . .
Grace Creek	May 13	4	2.0	8.0	70	. . .
Seventeen Creek	May 13	2	8.0	15.0	35	. . .
Little Black River	May 14	28	5.0	10.0	897	. . .
Trout River	May 16	79	5.0	14.0	1,887	10[1]
Carp Creek[2]	May 25	15	5.0	10.0	300[3]	11
Swan River	May 26	62	8.0	14.0	2,444[4]	18
Greene Creek	May 31	4	3.0	10.0	48	. . .
Squaw Creek	June 11	3	8.0	17.0	72	. . .
Middle Lake	June 12	6	9.0	17.0	144	. . .
Munuscong River[2]	June 17	40	3.0	6.0	1,980	5
Little Munuscong River[2]	June 20	27	3.0	6.0	306	. . .
Tawas Lake Outlet	June 25	130	7.0	13.0	2,394	. . .
Sims Creek	June 26	4	9.0	14.0	90	. . .
Total	. . .	456	. . .	. . .	11,436	44

[1] 200 pounds of heavy granules of 5-percent Bayer 73.

[2] Re-treatment.

[3] 231 pounds of 3,4,6-trichloro-2-nitrophenol and 69 pounds of 2,5-dichloro-4-nitrophenol.

[4] Includes 1,011 pounds of 3,4,6-trichloro-2-nitrophenol and 303 pounds of 2,5-dichloro-4-nitrophenol.

applications of chemical. Carp and Schmidt Creeks and Trout River each contained a lake in their system and needed individual treatment of each section; Swan Creek contained 2 lakes that divided the stream into three sections.

Budget restrictions curtailed all sea lamprey control as of July 1 on Lake Huron tributaries. Thirty of 51 streams known to contain sea lamprey were treated once and 3 were treated a second time. Seven of the 18 untreated streams contain large populations of sea lamprey ammocetes. The 7 are the Ocqueoc, Devils, Au Sable, East Au Gres, Au Gres, and Rifle Rivers, and Silver Creek.

Movement of tagged sea lampreys in the Great Lakes

Tags have been recovered from 289 of the 1,792 sea lampreys tagged and released in the fall of 1966 and spring of 1967. Two sea lampreys tagged and released at Sault Ste. Marie were captured at electric barriers on the Ocqueoc River and Echo Lake Outlet, Lake Huron. In Lake Superior, a sea lamprey tagged and released at Traverse Bay was captured in the Iron River weir, and 1 tagged and released in eastern Lake Superior was taken in the Brule River in western Lake Superior. A recently metamorphosed sea lamprey that was dye-marked and released in the Ocqueoc River, Lake Huron, on March 14, 1966, was captured at the electric barrier on the Manitou River, Lake Huron, on July 28, 1967.

Interlake dispersion of tagged sea lampreys was as follows: 18 tagged at St. Ignace (Lake Huron) were captured in Lake Michigan; 3 tagged in northern Lake Michigan were captured in Lake Huron; and 2 tagged in the St. Marys River were captured in Lake Superior.

Numbers of sea lampreys observed by commercial fishermen in St. Martins Bay, Lake Huron, near St. Ignace, were greatly reduced in July and August. In September, however, small lampreys were reported as numerous as in previous years. All the larger streams in this area producing parasitic-phase lampreys were treated in 1966. Apparently sea lampreys from streams of other areas have moved into St. Martins Bay. Monitoring of the fishery and tagging of sea lampreys were discontinued on July 1 because of a reduction in funds.

Re-establishment in treated streams

Re-established populations of sea lampreys were present in 23 streams of Lake Superior in 1967. The 1963 year class was present in 2 streams, the 1964 year class in 5, the 1965 year class in 8, the 1966 year class in 10, and the 1967 year class in 14.

Sea lamprey larvae were recovered in 3 small streams in Chippewa County that previously had not harbored re-established populations of sea lampreys for 4 or more years. In Naomikong Creek, one 20-millimeter ammocete (1967 year class) was recovered. No ammocetes were recovered in this stream in the 5 years, 1962-66. In Ankodosh Creek, a 65-millimeter larva, presumably of the 1965 year class, was collected. No other year classes were recovered in this stream during the 7 years, 1961-67. Two larvae, 48 and 54 millimeters, of the 1966 year class, were recovered in Galloway Creek. The 1966 year class is the only one re-established in Galloway Creek during the 6 years, 1962-67.

The reduction in the number of spawning sea lampreys captured at the electric barriers since 1961 was accompanied by a decline in the number of streams infested with young of the year and the mean number recovered per hour (Figure 1). The mean number of young of the year is measured by the rate of recovery per hour with an electric shocker at index stations in 9 streams. In 1966, the number of larvae recovered declined 83 percent and the number of streams infested declined 58 percent from the peak year of 1961.

Information collected from the Sturgeon River, Baraga County, indicates that sea lampreys may transform within 2 years. To substantiate the findings and provide additional evidence of metamorphosis at an early age, a study was initiated to provide data on growth and initial metamorphosis of ammocetes in the Sturgeon River. A total of 531 adult sea lampreys was tagged and released in the Sturgeon River in 1967 to establish a known-age year class. Although none of the tagged lampreys were recovered and only 11 nests were counted, young-of-the-year ammocetes are present in sufficient numbers to trace their growth. By mid-September the mean length of the larvae was 22 millimeters and in October the length had increased to 28 millimeters.

Re-establishment studies were terminated in Snyder-Deadhorse Creek and Hog Island Creek, tributaries to northern Lake Michigan, when the streams were treated, 7 years after the establishment of the 1960 year class of sea lampreys. The recovery of a recently metamorphosed sea lamprey in Snyder-Deadhorse Creek, prompted the treatment of the streams. The 2 streams were monitored annually for growth and relative abundance of ammocetes. Two metamorphosed sea lampreys

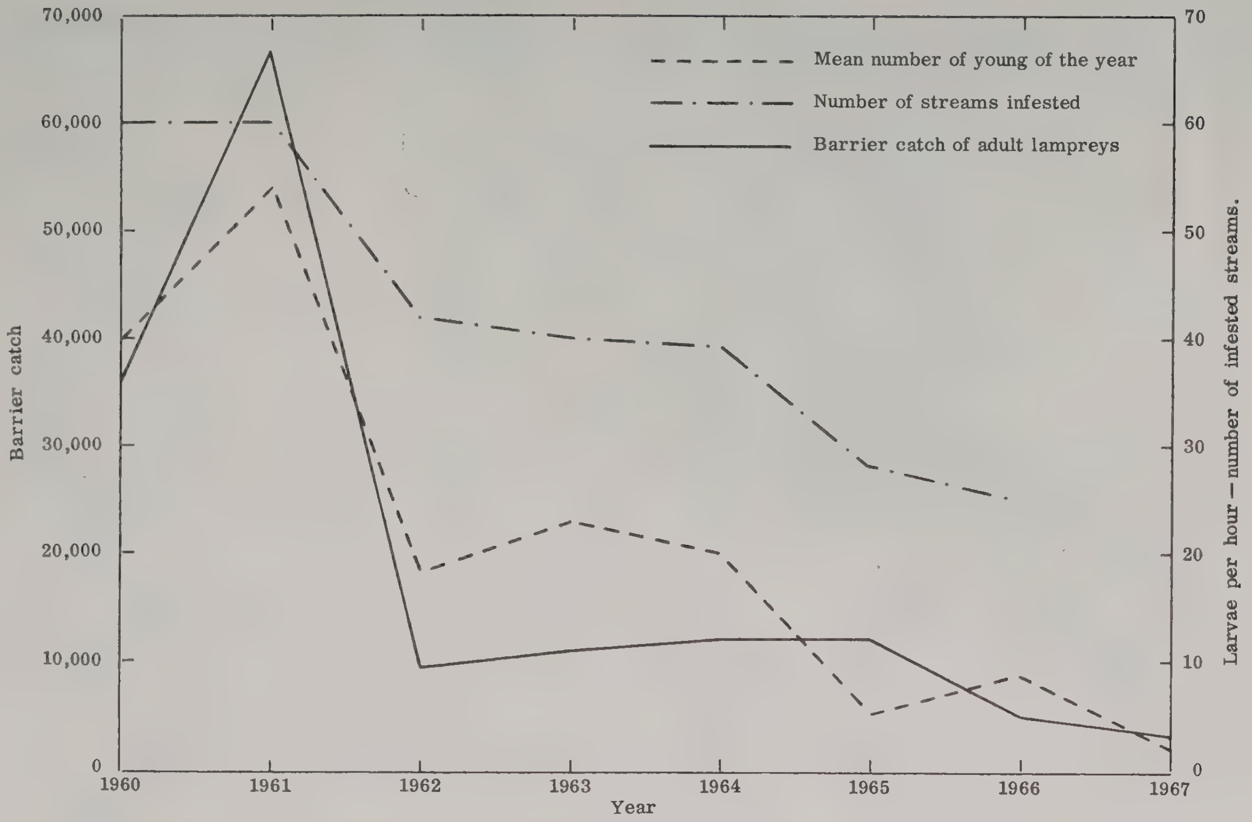

Figure 1.—Relation between the mean number of young of the year sea lampreys recovered per hour with electric shockers in 9 streams, the number of streams infested with young of the year, and the catch of adult sea lampreys at electric barriers on 16 index streams by year on the south shore of Lake Superior, 1960-67.

were collected in Snyder-Deadhorse Creek and 1 recently metamorphosed lamprey was recovered in Hog Island Creek. The ammocetes in the 2 streams were concentrated within the 1/4 mile of stream just above the mouth. The data show that a small and insignificant percentage of the sea lampreys begin metamorphosis in 7 years in the 2 streams.

The growth rate of re-established populations of sea lamprey larvae is being monitored in selected streams where age groups are distinct due to rapid growth or the absence of other year classes. The mean length of age-IV sea lampreys re-established in 1963 in the Mosquito River was 98 millimeters in September. This rate of growth parallels the growth of the known-age population in the Big Garlic River. In contrast, age-II larvae from the 1965 year class in the Bad River have attained a mean length of 105 millimeters. The Waiska River has an isolated year class which grew at a rate intermediate to that of lampreys in the Mosquito and Bad Rivers. Sea lampreys marked in May 1966 as age-II larvae in the Salmon-Trout River, Houghton County, were recovered during chemical treatment in August 1967 as age-III larvae. Fifty-four percent of the marked larvae were recovered and all were taken within 100 feet of the release site. The mean length of the larvae increased from 80 millimeters (range 61-110 millimeters) at marking to 144 millimeters (range 127-160 millimeters) at recovery. The annual growth of the ammocetes averaged 48 millimeters for the 3-year period—one of the most rapid growth rates recorded in Lake Superior tributaries. The ammocetes were in the length range where metamorphosis takes place, but no metamorphosed sea lampreys were found.

Lake-dwelling ammocete populations

A reduction in funds necessitated termination on July 1 of the project to monitor ammocetes in estuaries and inland lakes. The electric beam trawl was used before July 1 to survey areas in Lake Superior and northern Lake Huron. No sea lamprey ammocetes were collected in Lake Superior. Sea lamprey ammocetes were collected in northern Lake Huron off the mouths of Albany Island, Trout, and Nuns Creeks, and the Carp River. Rate of capture of sea lamprey larvae off the mouth of the Carp River increased from 2.8 per 100 minutes of tow time after treatment of the area with Bayer 73 in October 1966 to 66.7 per 100 minutes in June 1967. Failure to recapture any of the 1,000 ammocetes marked and released before chemical treatment in 1966 indicated a successful treatment of the area. Apparently the increase in number of larvae captured off the mouth of the Carp River in June, 1967, was caused by immigration.

Lamprey population assessments

Assessment surveys were completed on 30 index streams in 1967 (9 each on Lakes Superior and Huron, and 12 on Lake Michigan). Twenty-five streams were checked for the first time this year and 5 were re-surveyed after initial examinations in 1966. Recovery of sea lamprey larvae of all lengths ranged from 88 per hour on Silver Creek on Lake Huron to none on the Two Hearted River on Lake Superior. Abundance of ammocetes apparently varied according to the natural productivity of the stream and to the number of year classes of ammocetes present. Yields were generally lowest from recently treated Lake Superior streams with control barriers, and highest from untreated Lake Huron tributaries without barriers.

The number of sea lamprey larvae increased noticeably at similar stations on 2 of the 5 index streams initially examined in 1966. The catch of sea lamprey ammocetes from 6 stations on the Platte River was 12.4 per hour this year compared with 9.5 per hour last year. Capture rates increased from 2.4 per hour to 5.5 per hour on 27 stations on the Pere Marquette River. The other streams that had been initially surveyed in 1966 were later treated, and 1967 surveys revealed mostly small re-established populations.

Although information from these first assessment surveys has little value regarding recent changes in lamprey populations, it does provide a basis for comparing results of subsequent surveys and perhaps determining trends in future abundance of larvae.

Sea lamprey research

The Hammond Bay Laboratory was concerned primarily with the development of larvicides, particularly those containing mixtures of TFM and Bayer 73. The chemicals have also been tested as an irritant to cause emergence of larval lampreys in surveys. Research has continued on the life history and physiology of ammocetes.

Development of larvicides. Studies of the usefulness of Bayer 73 in a synergistic mixture with TFM for lamprey control demonstrated that a 2-percent addition, by weight, of Bayer 73 to TFM reduced larvicide requirements by about 50 percent without lowering selectivity below an acceptable level. Results of bioassays with this mixture were consistent in the laboratory and were reproduced in flowing-water raceway tests. The 2-percent mixture used in the field, however, produced fish kills that were completely unpredictable from pretreatment bioassays. Most of the streams were tributary to lower Lake Michigan. The mixture has been used more successfully in the softer waters of the Lake Superior watershed and in some streams tributary to northern Lake Michigan.

Additional studies were designed to define more closely the toxicity of TFM, Bayer 73, and several proportions of the 2 compounds. Inquiry also was made into the effect of water quality on synergistic action and the proper mixtures for use in waters of different qualities. The following observations on toxicity and selectivity have been made:

1. Regardless of species, test chemical, or mixture, the toxicity of the chemicals decreased with increased water alkalinity.
2. Increasing the proportion of Bayer 73 to TFM in the mixtures caused increased toxicity to all species, regardless of alkalinity.
3. Selectivity generally decreased with increased percentages of Bayer 73, although not with all species.
4. The amount of Bayer 73 needed to produce a 50-percent increase in toxicity over TFM alone varied with the dilution waters. In the least alkaline water a 4-percent addition was required; a 2-percent addition produced the same results in more alkaline waters. An 0.5-percent addition has consistently given a 35- to 40-percent increase in toxicity in test waters averaging 170 ppm in total alkalinity and has shown little or no loss in selectivity compared to TFM alone.

A satisfactory measurement of the synergistic action between TFM and Bayer 73 has not yet been possible. It appears, however, that the synergistic action between the 2 compounds is greater in waters with higher alkalinity. The interaction between the chemicals would tend to compound any adverse effect that would occur from improper concentrations. Domestic, industrial, and thermal pollution, presence of pesticides, and dense and varied fish populations, are factors that may complicate treatment of tributaries to lower Lake Michigan. On the basis of our present knowledge, the following mixtures of TFM and Bayer 73 are recommended for treating streams:

Total alkalinity (ppm)	Percent Bayer 73
25 - 50	3.0
50 - 100	2.0
100 - 150	1.0
Over 150	0.5

Search for irritants. The testing of chemicals to determine their potential to cause irritation and emergence of larval lampreys is continuing. Compounds are first screened to determine their toxic level to fish and larval lampreys and then re-tested at levels nontoxic to fish to determine if they cause emergence of larvae within 24 hours. No promising chemicals were found among the approximately 1,400 tested.

Downstream lamprey migration in the Ocqueoc River. Fyke nets fished continuously in the Ocqueoc River for the past 5 years provided data on the characteristics and magnitude of downstream-migrating lampreys that will be valuable in determining the effectiveness of future chemical treatments. A single net has been fished continuously in the same location since 1963-64. The catch in this index net was 3,373 in 1963-64, 1,174 in 1964-65 (the net was lost during extremely high water in the spring), 3,913 in 1965-66, 3,248 in 1966-67, and 2,179 for the first half of the 1967-68 migrational year. To evaluate the efficiency of the index net and to provide a basis for calculating total downstream runs, mark-recapture studies were initiated during the 1963-64 migration. The number of downstream migrants was estimated at 42,000 in 1963-64; 57,000 in 1965-66; and 80,000 in 1966-67.

Starting with the 1965-66 runs, information has been collected on length frequency and sex ratios of downstream migrants. In 1965-66, the average length of 4,018 downstream migrants was 139.9 millimeters (range, 104-188 millimeters). The females averaged about 4.9 millimeters longer than the males. The percentage of males was 40.4 percent. In 1966-67, the average length of 2,571 downstream migrants was 144.9 millimeters (range, 109-198 millimeters). The females averaged about 6.6 millimeters longer than the males and the percentage of males was 44.4 percent.

Blood studies. A study was begun in 1966 to determine normal blood values for the various stages of the sea lamprey and to determine whether the time of metamorphosis can be predicted from ammocete blood values. Only red blood cells were studied because white blood cells could not be identified positively and counted accurately. The hematocrit, hemoglobin content, and erythrocyte count were determined for larval, metamorphosing, and adult sea lampreys. All the blood values in ammocetes increased with length. During morphological transformation the blood values decreased but increased as the adults began to feed. The mean blood values for mature adults are similar to those of ammocetes. At spawning, males exhibit higher blood values than do females. Hemoglobins have been separated electrophoretically at five stages of the sea lamprey's life cycle: larva, transforming individuals before downstream migration, recently transformed downstream migrants, parasitic lampreys, and fully mature spawning adults.

Experimental population of ammocetes. Ammocetes of the 1960 year class (now age-group VII) established in 1960 in the Big Garlic River, Marquette County, Michigan, metamorphosed for the third successive year. The all-season trap captured 223 metamorphosed lampreys in 1967. Of these, 2 were taken in April and were the first spring migrants captured. The trap captured 44 young adults in 1966 and 4 in 1965. The young parasitic lampreys ranged from 127 to 180 millimeters long and averaged 151 millimeters. The percentage of males was 40 percent in 1967 compared with 51 percent in 1966.

The catches of ammocetes in the all-season trap decreased in 1967. The trap captured 7,572 in 1967, 7,925 in 1966, 4,336 in 1965, 2,847 in 1964, 370 in 1963, and 9 in 1962. The percentage of males among ammocetes over 100 millimeters was 27 percent in 1967, 21 percent in 1966, and 19 percent in 1965. The annual growth rate of ammocetes continued to decrease. The mean length of 470 ammocetes was 113 millimeters (range, 72-165 millimeters), an increase of only 2 millimeters from 1966 (Table 7).

Since October 1962, 10,006 ammocetes have been marked and returned to the study area. Of the 419 marked lampreys recovered in 1967, 164 were recently metamorphosed. Ammocetes marked in 1962 still retain visible marks after 5 years. Marks on metamorphosed lampreys are obscured by pigment and difficult to detect. All parasitic-phase lampreys were dissected and examined for subcutaneous marks.

Table 7. Growth of 1960 year class of ammocetes in the Big Garlic River to October, 1967

Year	Mean length (mm)	Length range (mm)	Length increment (mm)
1960	13	10- 19	13
1961	39	25- 54	26
1962	63	37-107	24
1963	80	52-134	17
1964	92	43-159	12
1965	107	65-176	15
1966	111	67-179	4
1967	113	72-165	2

Adult sea lampreys bypassed the downstream trap in June through a channel opened by flood waters. The upstream migration of these lampreys was limited by a natural barrier to the lower 1-1/2 miles of the 5-mile study area. Four nests were located in the study area and 7 of the escaped adults were captured at the trap. The young of the year averaged 15 millimeters long (range, 11-18 millimeters). The growth of this population and its influence on the age-VII larvae will be studied. A downstream trap was constructed in the bypass channel to prevent further escapement and to monitor any downstream movement of ammocetes and parasitic-phase lampreys.

Final data were collected on the staging of external metamorphosis of sea lamprey from the Big Garlic River. Five morphologically distinct stages and the period of time for metamorphosis were determined. Stages were based on development of the eye, oral fringe, sensory pores, mouth, and teeth. A sequence of metamorphosing lampreys was preserved to determine accompanying histological changes.

PAUL E. SMITH, ROBERT C. COUNTS,
and ROBERT I. CLUTTER

CHANGES IN FILTERING EFFICIENCY OF PLANKTON NETS DUE TO CLOGGING UNDER TOW

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By

PAUL E. SMITH, ROBERT C. COUNTS, and ROBERT I. CLUTTER

Bureau of Commercial Fisheries
California Current Resources Laboratory
La Jolla, California, USA

The problem of clogging is inherent in sampling plankton and this paper reports a study of clogging rates in tests of design variables of plankton nets, such as mesh size, filtering area, and net form. Telemetering flow meters were used to determine the effects of these variables on the rate of clogging of pairs of plankton nets under tow in waters of different clarity. Metering of flow is necessary for evaluating clogging. A water clarity measurement is not useful for predicting clogging rate and the gross appearance of the net after the tow is not necessarily a reliable indicator of whether clogging has lowered filtration efficiency during the tow. Fine mesh nets with comparable mesh aperture area filter as well initially as do nets with larger apertures but clog much more rapidly. Compared to silk with mesh apertures 0·550 mm wide, nylon with apertures 0·333 mm, 0·201 mm and 0·101 mm wide clog 3, 5 and 35 times as rapidly. In the cylinder-cone nets of 0·333 mm nylon mesh, the volume filtered at more than 85% efficiency was increased six-fold by doubling the filtering area. An equation describing the relation of the ratio of filtering area to mouth area for 0·333 mm nylon is:

$$\log_{10} R = 0{\cdot}38 \log_{10} \frac{V}{A} - 0{\cdot}17$$

where R is the ratio of filtering area to mouth area, V is the volume to be filtered and A is the mouth area of the net. The cylinder and cylinder-cone nets were superior in sustained filtration efficiency to cone-shaped nets. We attribute this advantage to the oscillations of the cylindrically placed mesh which tend to clean the mesh at a higher rate. An example is given of the method by which a new net was designed to lessen the probability of clogging.

INTRODUCTION

> "... Four places of decimals in a computed coefficient can hardly offer compensation for an error so fundamental as the variation in the straining capacity of the net".
>
> KOFOID (1897)

Intensive studies of productivity on traditional fishing grounds have elicited continuing interest in the problems of sampling zooplankton since HENSEN

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initiated quantitative plankton sampling in the 1890's. The problem of clogging is inherent in the process of sampling plankton and remains to be fully evaluated. This paper reports a study of clogging rates in tests of design variables of plankton nets, such as mesh size, filtering area, and net form, under differing field conditions.

Hensen (1895) carried out filtering experiments on silk meshes of several sizes to determine the amount of filtering area required to allow water to pass efficiently into the net. Although he recognized that clogging of the mesh apertures reduced filtration, he reasoned that "... in the worst cases not more than 5% of the net could be affected and usually much less ..." (p. 101). Kofoid (1897) demonstrated the importance of clogging under certain conditions. Reighard (1897) suggested that the problem of estimating the volume filtered could be most simply solved by installing a flow meter in the mouth of the net.

Langford (1953) emphasized that even though the total volume filtered could be closely estimated, the tow did not equally represent all parts of the water column through which the net was drawn if clogging occurred during the tow. During calibration trials, Yentsch and Duxbury (1956) noted that the flow meter of a Clarke-Bumpus sampler filtering lake water stopped after 4 to 8 minutes with mesh aperture widths of 0·07 mm and after 15 minutes with a 0·12 mm aperture net. Tranter and Heron (1965) found that the filtration efficiency of the Australian modification of the Clarke-Bumpus sampler decreased from 75% to 45% in 10 successive tows of 17 m in a hydraulic test channel.

In addition to causing misrepresentation of the water column, progressive clogging has two secondary effects on the accuracy of sampling. First, clogging some mesh apertures increases pressure from the inside to the outside of the net through the remaining open apertures. Hensen (1895) said that this pressure increased the probability of the extrusion of small or soft-bodied organisms. Second, as clogging proceeds, the impermeability of parts of the net forces water to bypass the net mouth. Partial rejection of water by a net propagates a turbulent front of water ahead of the net which may be detected by zooplankters (Fleminger and Clutter, 1965). The rate of clogging may be expected to change regionally and seasonally and thus make more variable the errors caused by avoidance, the loss of organisms through the meshes and misrepresentation of the water column.

METHODS

The tests reported here were conducted from the R.V. "Black Douglas" of the California Current Resources Laboratory of the Bureau of Commercial Fisheries, La Jolla, California, at the following sites: just offshore of the breakwater at San Pedro, California (33° 45′ N, 118° 15′ W), 8.–9. October ("San Pedro I") and 13.–14. October ("San Pedro II"); offshore from Santa Catalina Islands (33° 25′ N, 118° 20′ W), 10.–12. October 1965. The San Pedro and Catalina sites were selected for marked differences in water clarity. Secchi disc readings were taken with a newly painted white weight with a diameter of 30 cm. Several clarity estimates were made each day.

DEFINITION OF TERMS

Several terms are used in this report to describe plankton nets, their mesh and their filtration performance as follows:

1. *Mesh size*

The width of the mesh aperture in millimeters. The commonly used standard sieve numbers, manufacturers' grades, and meshes per inch or centimetre do not translate easily to mesh size and it is suggested that their use be discouraged.

2. *Mesh area*

The total area of the completed net, to include the mesh apertures and filaments (expressed in square metres).

3. *Porosity*

That fraction of the mesh area which is open. This can be determined by planimetry of photographs or drawings of mesh or, in the case of monofilament nylon meshes, by the equation:

$$1)\ B = \frac{a^2}{(a+f)^2}$$

B = Porosity
a = Aperture width, and
f = Diameter of the filament

4. *Filtering area*

The product of porosity times mesh area (expressed in square metres).

5. *Filtering area ratio*

The ratio of filtering area to mouth area calculated by the following equation:

$$2)\ R = \frac{\text{filtering area}}{\text{mouth area}}$$

6. *Filtration efficiency*

The percentage of the water encountered which is filtered after passing through the mouth of the net. It is determined by the equation:

$$3)\ F = \frac{\text{Volume of water filtered}}{\text{Volume of water encountered}} \times 100$$

In practice this value is determined indirectly by comparing the velocities inside and outside the mouth of the net. The term is the reciprocal of filtration coefficient (HENSEN, 1895).

In every test, two nets with a mouth diameter of 1 m were mounted, one at each side of a 1 × 3 m rectangular steel frame. Nets 4 and 7 (Table 1) are similar in dimensions to a net described by AHLSTROM (1948, Figure 4). Net 4 had a mesh size of 0·333 mm nylon (NITEX*), and net 7 had a mesh size of 0·550 mm silk mesh (AHLSTROM, 1954). The silk net has been the "standard" net in surveys made by the California Cooperative Oceanic Fisheries Investigations (CalCOF I) since the beginning of the work in 1949 (Marine Research Committee, 1955). The 0·333 mm nylon net was chosen as a reference net for

TABLE 1. Description of plankton nets tested for clogging rate

Net #	Form	Mesh material	Mesh size (mm)	Porosity	Filtering area (m²)	R^1	Total length (m)
1	Cone	Nylon	0·333	0·46	2·50	3·2	3·1
2	Cone	Nylon	0·333	0·46	3·75	4·8	4·7
3	Cylinder-cone	Nylon	0·333	0·46	2·50	3·2	2·5
4[2]	Cylinder-cone	Nylon	0·333	0·46	3·75	4·8	3·8
5	Cylinder-cone	Nylon	0·333	0·46	5·00	6·4	5·1
6	Cylinder-cone	Nylon	0·571	0·49	3·75	4·8	3·6
7[3]	Cylinder-cone	Silk	0·550	0·36	2·50	3·2	3·3
8	Cylinder-cone	Silk	0·550	0·36	3·75	4·8	4·9
9	Cylinder-cone	Silk	0·450	0·34	3·75	4·8	5·2
10	Cylinder	Nylon	0·333	0·46	1·25	1·6	1·4
11	Cylinder	Nylon	0·333	0·46	2·50	3·2	2·2
12	Cylinder	Nylon	0·333	0·46	3·75	4·8	3·1
13	Cylinder	Nylon	0·333	0·46	5·00	6·4	4·0
14	Cylinder	Nylon	0·201	0·43	5·00	6·4	4·2
15	Cylinder	Nylon	0·101	0·36	5·00	6·4	4·9
16	Cylinder	Silk	0·550	0·36	5·00	6·4	4·9

[1] $R = \frac{\text{Filtering Area}}{\text{Mouth Area}}$

[2] Nylon in CalCOF I net form.

[3] Standard CalCOF I net.

clogging because this mesh size had been recommended as an interim standard net (Biological Methods Panel Committee on Oceanography, 1964). The other 14 nets were designed specifically to test the effects of different mesh sizes, filtering areas and net forms on the rate of clogging and the duration of efficient filtration.

Three net forms were tested: cone, cylinder-cone and cylinder. Each cone net tapered evenly from a mouth of 1 m diameter to its cod end. Each cylinder-cone net had an anterior cylinder with a diameter of 1 m, which contained 40% of the total filtering area, followed by a cone tapering to the cod end. The cylinder nets had all their mesh in the cylinder which was followed by a short nonfiltering cone made of dacron sailcloth tapering to its cod end. All cod ends had a diameter of 0·10 m. All nets had dacron webbing 2·54 cm wide along their lengths to strengthen them. The cone and cylinder-cone nets had 8 longitudinal ribs; the cylinder nets had 9. Three ribs in the longest cylinder nets (13, 14, 15 and 16, Table 1) had a 2·3 mm cable sewn into the seams for additional support.

The filtering area of the standard CalCOF I net (7, Table 1) is about 2·5 m² which is 3·2 times the mouth area of 0·7854 m² ($R = 3{\cdot}2$). A nylon net with a mesh size of 0·333 mm (net 4, Table 1) and with the same dimensions has 3·75 m² filtering area and an R of 4·8 times the mouth area. This is explained by the difference in porosity which is 0·46 for this nylon mesh size and is 0·36 for the silk mesh after shrinkage and use. In the design of the other 14 nets, the filtering areas were adjusted to 1·25, 2·50, 3·75 and 5·00 m² and R thus equalled 1·6, 3·2, 4·8 and 6·4. In addition to the 0·333 nylon and 0·550 mm silk meshes, tests were made with nylon meshes of three additional sizes, 0·101, 0·201, and 0·571 mm, and one silk net with a mesh size of 0·450 mm. The latter silk net was tested for clogging rate but as yet has not been used enough

TABLE 2. Water clarity estimates by Secchi Disc

Sites, Dates and Tows	Number	Secchi depth in metres Maximum	Median	Minimum
San Pedro I 8. and 9. October Tows 1–14	15	6·5	4·5	3·5
Catalina 10., 11. and 12. October Tows 15–31	21	30	24	19
San Pedro II 13. and 14. October Tows 32–38	12	7·0	6·25	4·5

to permit comparison with nylon or shrunken silk. It is predicted that after more use, its mesh apertures will be reduced to a size approximately the same as that of the 0·333 mm nylon mesh. Water flow through each of the paired nets was monitored by a ducted flow meter (Marine Advisers model B-7) mounted 15 cm from the net rim and on the same plane as the rim. Unimpeded flow was measured by a similar meter mounted in the central open space between the two nets. Permanent magnets embedded in the margins of the 5 impeller blades, depressed a reed switch 5 times each revolution to complete a low voltage electrical circuit. The number of switch contacts in 10 seconds was simultaneously accumulated on an electronic event counter (HEWLETT-PACKARD, model 5211 b) for each of the three meters. The reading for each flow meter was converted to m/sec by calibration constants.

The instantaneous filtration efficiency (F_i) was calculated as a percentage by comparing the velocity of the water within or "accepted" at the net mouth (U_a) with the velocity of water at the free stream meter, *i.e.* "presented" to the net mouth (U_p) by the formula:

$$F_i = \frac{U_a}{U_p} 100$$

The volume of water accepted by the net (V_a) as well as the volume presented to the net (V_p) was estimated by the following formulas:

$$V_a = A\,(U_{a_1} t_1 + U_{a_2} t_2 + U_{a_3} t_3 + \ldots\ldots + U_{a_n} t_n) \qquad (3)$$

$$V_p = A\,(U_{p_1} t_1 + U_{p_2} t_2 + U_{p_3} t_3 + \ldots\ldots + U_{p_n} t_n) \qquad (4)$$

Where A is the area of the net mouth (0·7854 m^2 in this study), t is the time interval represented by a particular velocity reading, and n is the last velocity reading of interest.

The net was considered to be clogged when water acceptance fell, and remained, below 85%. Two measures of sustained filtration efficiency were calculated for these tests; 1) the time that filtration efficiency was 85% or more and, 2) the volume of water which had been filtered at 85% or greater efficiency. The filtration efficiency of all nets but one initially was greater than 85% and ranged as high as 95%. One net (10, Table 1) was designed to be less efficient than 85% by constructing it with an R of 1·6.

Cable length needed for telemetry restricted tows to the upper 10 m of water, but the nets were always below and outside the turbulent influence of the ship's wake. Mean towing speed was 1·13 ± 0·2 m/sec (2·2 ± 0·4 knots).

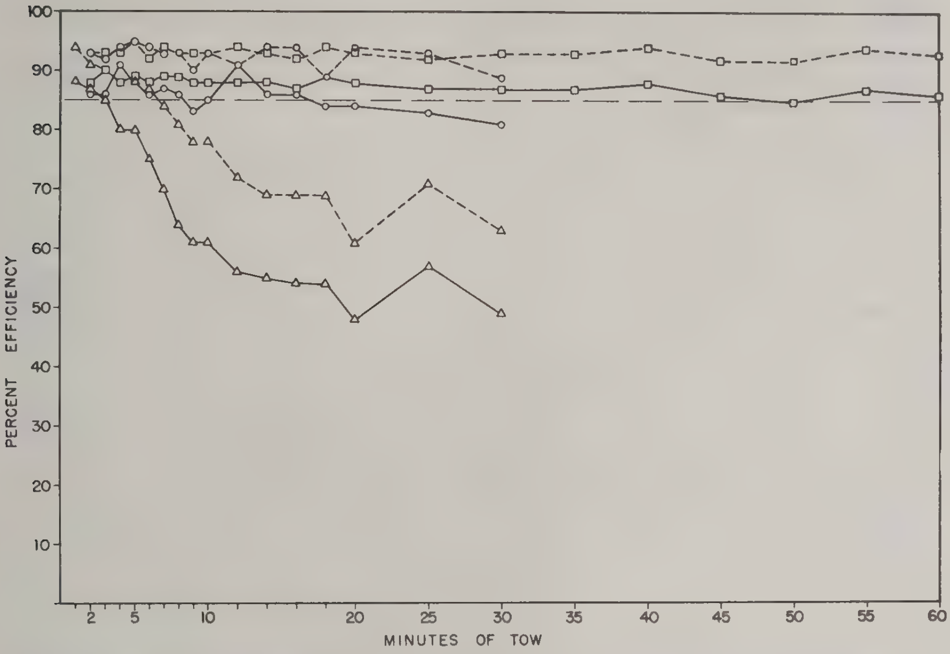


Figure 1. Net filtration efficiency – water clarity series. Three paired tows comparing two nets with 0·550 mm mesh aperture width, silk cylinder-cone. Nets number 7 (*R* = 3·2) and 8 (*R* = 4·8) (see Table 1) at three towing sites. Dashed line = efficiency criterion of 85 per cent. Triangle, Secchi depth 4·5 m, at San Pedro I, tow three, 8. October; square, Secchi depth 24 m at Catalina, tow 30, 12. October; circle, Secchi depth 6.25 m at San Pedro II, tow 32, 13. October. (See Tables 2 and 3).

FACTORS WHICH AFFECT CLOGGING RATE

Clogging rate was affected, in decreasing order of importance in these tests, by 1) the composition and density of suspended materials in the water, 2) mesh size, 3) the ratio (*R*) of filtering area to mouth area, and 4) the form of the net. Each of the nets designed for this study was clogged to a filtration efficiency below 85% and then returned to the initial efficiency by washing before each succeeding test.

THE EFFECT OF TOWING SITE ON CLOGGING RATE

Estimates of water clarity for the three test sites are summarized in Table 2. One pair of silk nets (7 and 8) was towed at the San Pedro I, Catalina and San Pedro II sites. In the relatively clear water off Catalina, neither of these nets clogged enough to lower filtration efficiency, even after being towed for 1 hour. At the San Pedro I site the silk net, 7, (*R* of 3·2) clogged in 4 minutes after filtering 194 m^3 water: the silk net, 8, (*R* of 4·8) clogged in 6 minutes after filtering 322 m^3 water. Five days later at San Pedro II net 7 clogged in 16 minutes after filtering 786 m^3 water and 8 had not yet clogged after filtering 1,465 m^3 water in 30 minutes (Figure 1).

Figure 2. Net filtration efficiency – mesh size series. Comparison of nylon cylinder nets, $R = 6{\cdot}4$, numbered 13, 14, and 15 (see Table 1).

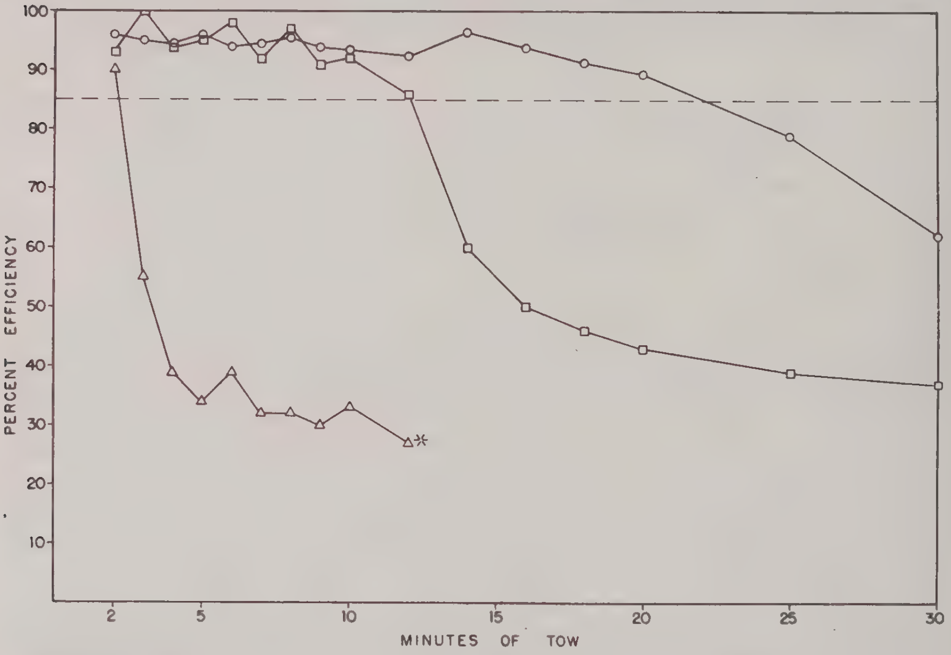


Figure 2A. Secchi depth 6·25 m at San Pedro, II 13. October (triangle, net number 15, 0·101 mm apertures, tow 36; square, net number 14, 0·201 mm apertures, tow 35; circle, net number 13, 0·333 mm apertures, combined results of tows 35 and 36).* Splitting of net number 15 prevented completion of the series.

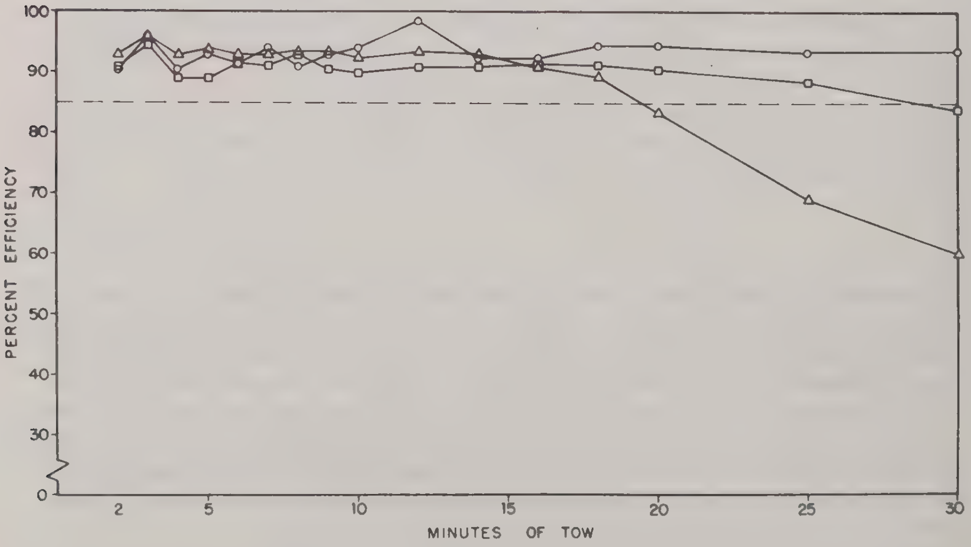


Figure 2B. Secchi depth 24 m at Catalina, 11. October (triangle, net number 15, 0·101 mm apertures, combined results of tows 23 and 25; square, net number 14, 0·201 mm apertures, combined results of tows 24 and 25; circle, net number 13, 0·333 mm apertures, combined results of tows 23 and 24).

Figure 3. Net filtration efficiency – mesh amount series. Comparison of nylon, cylinder-cone nets numbered 3, 4, and 5 (see Table 1).

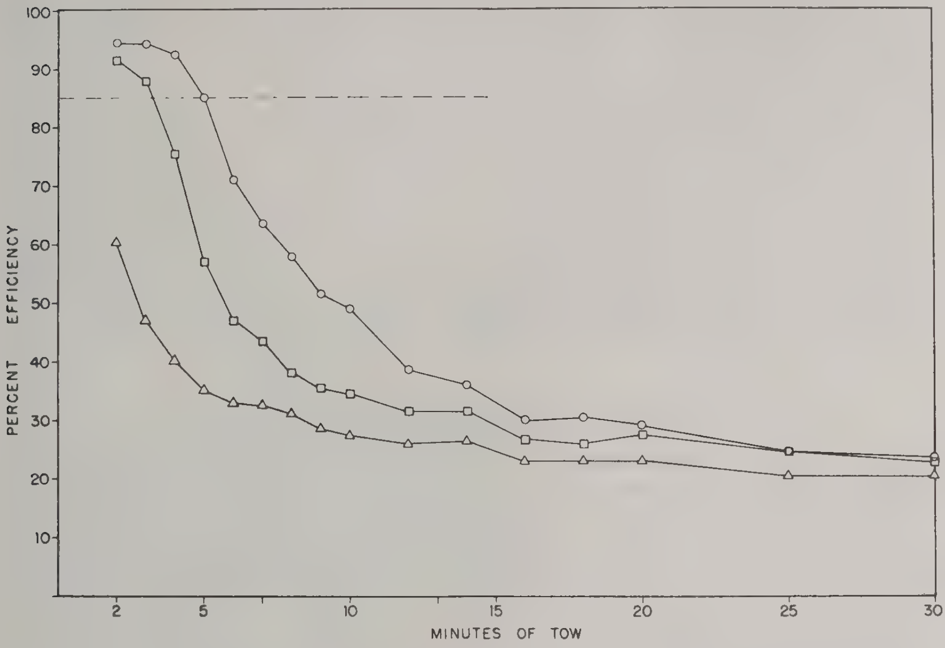


Figure 3A. Secchi depth 4·5 m at San Pedro I, 8. and 9. October (triangle, net number 3 $R = 3{\cdot}2$ combined results of tows 6 and 12; square, net number 4, $R = 4{\cdot}8$, combined results of tows 6 and 11; circle, net number 5, $R = 6{\cdot}4$, combined results of tows 11 and 12).

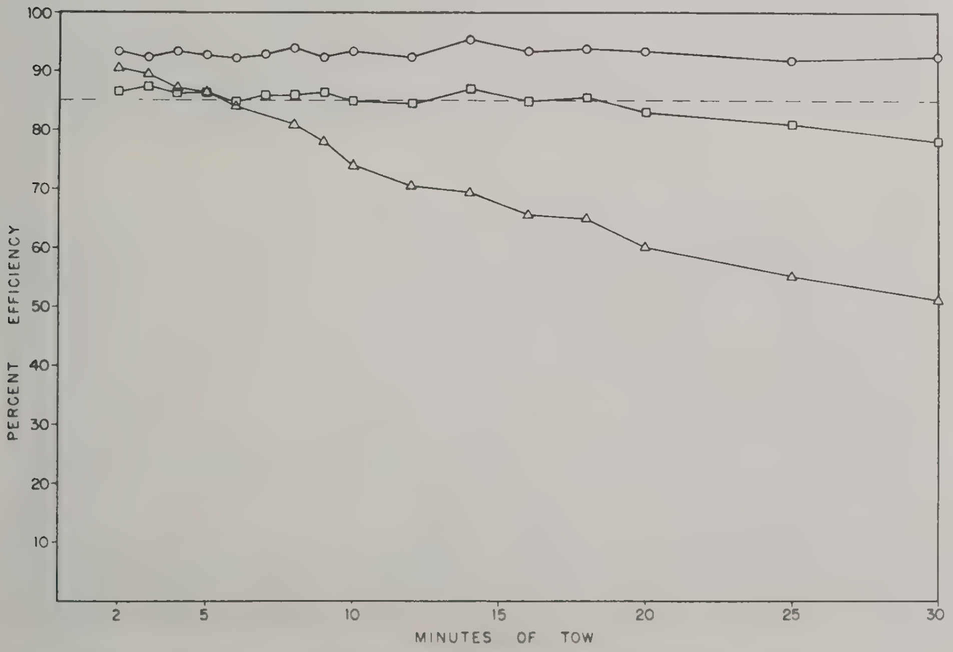


Figure 3B. Secchi depth 24 m at Catalina, October 10. and 11. (triangle, net number 3, $R = 3{\cdot}2$, combined results of tows 20 and 27; square, net number 4, $R = 4{\cdot}8$, combined results of tows 20 and 28; circle, net number 5, $R = 6{\cdot}4$, combined results of tows 27 and 28).

EFFECT OF MESH SIZE ON CLOGGING RATE

Fine mesh nets with comparable filtering areas, filter as well initially as nets with larger mesh sizes but clog more rapidly. Filtration efficiency versus time is shown in Figure 2 for three cylindrical form nylon nets, with mesh sizes of 0·101, 0·201 and 0·333 mm wide. Each net had an R of 6·4. In the turbid water off San Pedro II (Figure 2A) the 0·101 mm mesh net filtered at 90% efficiency for the first 2 minutes of tow and then clogged to less than 60% efficiency before the end of the third minute. The 0·201 mm net remained above 85% efficiency 12 minutes and then declined to 60% in the next 2 minutes. The 0·333 mm net retained high efficiency 20 minutes before declining to less than 85%. In the relatively clear water off Catalina Island (Figure 2B) all three nets maintained high efficiency for 18 minutes, after which the 0·101 mm net clogged to 83% at 20 minutes and the 0·201 mm net clogged to 84% at 30 minutes. The 0·333 mm net had better than 85% filtration efficiency during an hour of towing.

RELATION OF CLOGGING RATE TO FILTERING AREA

The period of efficient filtration is extended by the addition of filtering area to the net. Figure 3A and 3B show the results of three paired tows taken at each of two sites with nets of mesh size 0·333. The three nets had R's of 3·2, 4·8, and 6·4. To minimize the effects of small scale differences in clogging rate, each net was paired with each of the other nets in the series and the results for each net are the combination of two tows. The ratios of the volume of water filtered at greater than 85% were 1:2:4 at San Pedro I and 1:3:8 at Catalina for the three nets. Both ratios exceed the ratio of the filtering area in the nets (1:1½:2).

We attribute this effect to "self-cleaning" although we cannot determine whether the "cleaning" results from forcing clogging material through the apertures or its movement rearward inside the net. Figure 3A shows that the reserve mesh area of this form of net is inadequate for self-cleaning in extremely turbid waters. It should be noted that the 0·333 mm nets with an R of 6·4 in the A sections of Figures 2 and 3 are not comparable, even though both were at San Pedro, due to the different dates and clogging rates mentioned above.

EFFECT OF NET SHAPE ON FILTRATION EFFICIENCY

These tests showed that the conical net was inferior to the cylinder and cylinder-cone nets in the ability to maintain efficient filtration. The sustained-filtration relation between the cylinder and cylinder-cone nets was not established in these tests. At San Pedro the cylinder-cone filtered longer than the cylinder net (Figure 4A), but in the clear water off Catalina Island, the cylinder net filtered longer than the cylinder-cone net (Figure 4B). The ratio of volumes filtered above 85% efficiency through the cone, cylinder-cone and cylinder nets was 1:1·9:1·5 at San Pedro I and 1:2·0:3·9 at Catalina. In addition to the series in Figure 4 ($R = 4{\cdot}8$), five other paired tows compared nets of different form with other aperture ratios ($R = 3{\cdot}2$ and 6·4) in incomplete series. In the only comparison between cone and cylinder nets of ($R = 3{\cdot}2$), both nets clogged before 2 minutes but the cylinder net filtered 6% more water above 85% efficiency. The cylinder net was lost during this tow (nets 1 and II, tow 4, Table 3). The cone and cylinder-cone nets (1 and 3) of ($R = 3{\cdot}2$) were compared

Figure 4. Net filtration efficiency – form series. Comparison of 0·333 mm mesh aperture, $R = 4{\cdot}8$, nylon nets numbered 2, 4, and 12 (see Table 1).

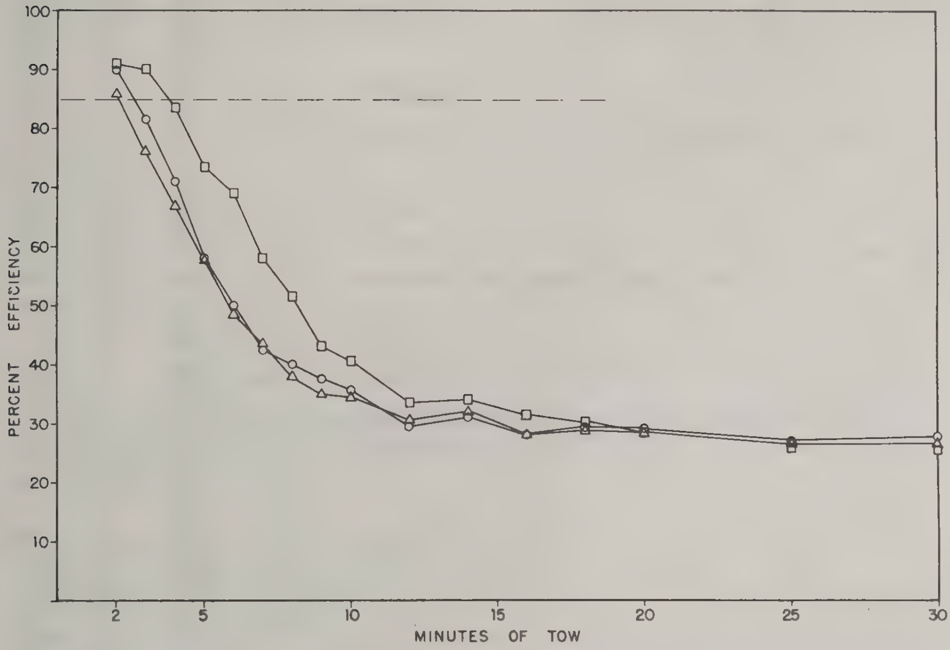


Figure 4 A. Secchi depth 4·5 m at San Pedro I, 9. October (triangle, net number 2, cone, combined results of tows 9 and 10; square, net number 4, cylinder-cone, combined results of tows 8 and 10; circle, net number 12, cylinder combined results of tows 8 and 9).

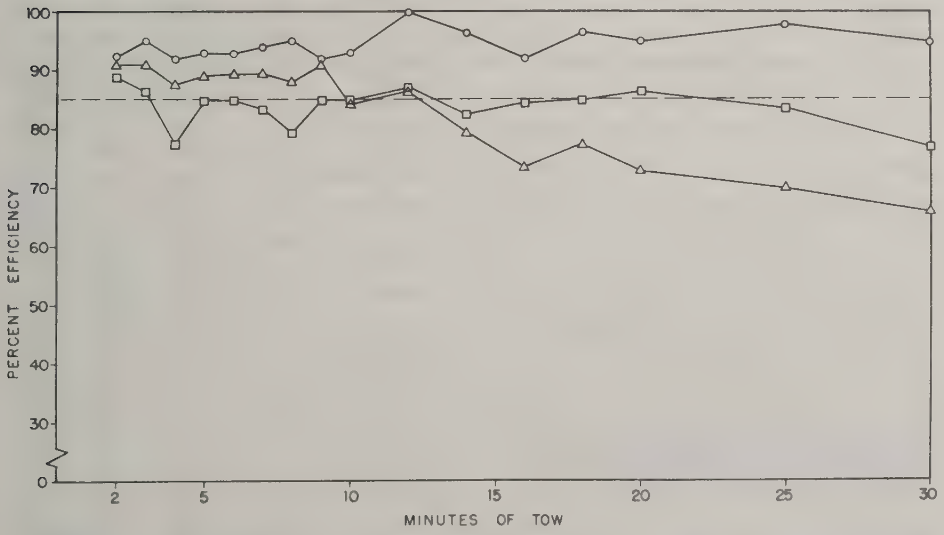


Figure 4B. Secchi depth 24 m at Catalina, 10. October (triangle, net number 2, cone, combined results of tows 17 and 19; square, net number 4, cylinder-cone, combined results of tows 18 and 19; circle, net number 12, cylinder, combined results of tows 17 and 18).

TABLE 3. Summary of all paired tows

Net	Site	Tow number	Volume[1] (m^3)	Time[2] (min)	Velocity (knots)
1. 3·2:1 0·333 mm Nylon Cone	San Pedro I	4	48	<2	2·6
		5	47	<2	2·4
		7	22	<2	1·9
	Catalina	21	87	<2	2·3
		22	137	3	2·2
2. 4·8:1 0·333 mm Nylon Cone	San Pedro I	7	79	3	1·9
		9	99	2	2·2
		10	88	2	2·1
	Catalina	17	459	9	1·8
		19	625	12	2·2
		22	542	10	2·2
3. 3·2:1 0·333 mm Nylon Cylinder-Cone	San Pedro I	5	49	<2	2·4
		6	43	<2	2·1
		12	65	2	2·1
	Catalina	20	292	5	2·1
		21	390	7	2·3
		27	441	8	2·3
4. 4·8:1 0·333 mm Nylon Cylinder-Cone	San Pedro I	1	121	3	2·1
		6	137	3	2·1
		8	123	3	2·0
		10	239	5	2·1
		11	115	3	1·9
	Catalina	18	1172	25	2·0
		19	962	20	2·2
		20	928	18	2·1
		28	1282	25	2·2
		29	1805	35	2·4
	San Pedro II	34	513	10	2·3
		38	600	10	2·6
5. 6·4:1 0·333 mm Nylon Cylinder-Cone	San Pedro I	11	178	5	1·9
		12	300	6	2·1
		13	375	8	1·9
	Catalina	26	2564	50	2·2
		27	>3188	>60	2·3
		28	2543	50	2·2
6. 4·8:1 0·571 mm Nylon Cylinder-Cone	San Pedro I	2	71	2	2·1
	Catalina	30	>3270	>60	2·2
	San Pedro II	33	1137	20	2·2
7. 3·2:1 0·550 mm Silk Cylinder-Cone	San Pedro I	3	194	4	2·2
	Catalina	31	>3210	>60	2·5
	San Pedro II	32	786	16	2·2
8. 4·8:1 0·550 mm Silk Cylinder-Cone	San Pedro I	2	317	7	2·1
		3	322	6	2·2
	Catalina	30	>3206	>60	2·2
		31	>3426	>60	2·5
	San Pedro II	32	>1465	>30	2·2
		33	>1456	>30	2·2
9. 4·8:1 0·450 mm Silk Cylinder-Cone	San Pedro I	1	238	5	2·1
	Catalina	29	>3069	>60	2·4
	San Pedro II	34	961	18	2·3
		38	1565	25	2·6
10. 1·6:1 0·333 mm Nylon Cylinder	Catalina	16	<61	<2	1·9
11. 3·2:1 0·333 mm Nylon Cylinder	San Pedro I	4	51	<2	2·6
12. 4·8:1 0·333 mm Nylon Cylinder	San Pedro I	8	103	3	2·0
		9	171	4	2·2
		14	88	2	2·1
	Catalina	15	1075	25	1·8
		16	>1331	>30	1·9
		17	2048	45	1·8
		18	2173	45	2·0

TABLE 3 (continued)

Net	Site	Tow number	Volume[1] (m³)	Time[2] (min)	Velocity (knots)
13. 6·4:1 0·333 mm Nylon Cylinder	San Pedro I	13	558	12	1·9
		14	207	5	2·1
	Catalina	15	>2391	>60	1·8
		23	2436	45	2·3
		24	>3419	>60	2·5
		26	>3033	>60	2·2
	San Pedro II	35	1430	25	2·3
		36	>778	>14	2·6
		37	1194	20	2·4
14. 6·4:1 0·201 mm Nylon Cylinder	Catalina	24	1506	25	2·5
		25	1601	30	2·3
	San Pedro II	35	654	12	2·3
15. 6·4:1 0·101 mm Nylon Cylinder	Catalina	23	1011	18	2·3
		25	1134	20	2·3
	San Pedro II	36	95	2	2·6[3]
16. 6·4:1 0·550 mm Silk Cylinder	San Pedro II	37	>3294	>60	2·4

[1] Volume filtered at greater than 85% efficiency.
[2] Towing time before efficiency decreased to below 85% efficiency.
[3] Net damaged.

at the San Pedro I and Catalina sites. At San Pedro both clogged before 2 minutes at which time the cylinder-cone had filtered 4% more water than the cone (tow 5). At Catalina (tow 21) the cone filtered 87 m³ and the cylinder-cone filtered 390 m³ before clogging. In seven tows that included cone nets, this type clogged faster than any cylinder or cylinder-cone net with which it was paired. Two tows compared the cylinder-cone and cylinder nets of ($R = 6·4$) (nets 5 and 13), one each at San Pedro I and Catalina. At San Pedro (tow 13) the cylinder-cone filtered 375 m³ and the cylinder 558 m³ before clogging. At Catalina the cylinder-cone filtered 2,564 m³ before clogging and the cylinder net had not yet clogged after filtering 3,033 m³ in 1 hour (tow 26). The cylinder filtered more water than the cylinder-cone before clogging in three of the four direct comparisons.

COMPARISON OF NETTING MATERIAL – SILK VS NYLON

Although comparisons of nets made of silk and nylon are recorded in Table 3, the results are not considered conclusive. The 40 XXX silk grit gauze had not yet shrunk to the size of 0·333 mm nylon mesh at the completion of the tests. Three comparisons were made between the 0·571 mm nylon net (6) and the 0·550 mm silk (8) net at the San Pedro I, Catalina and San Pedro II towing sites. At San Pedro I, the nylon net filtered 71 m³ in the 2 minutes before it clogged (tow 2). At Catalina, neither net had clogged at the end of a 1 hour tow (tow 30). At San Pedro II, the nylon net clogged after filtering 1,137 m³ in 20 minutes but the silk net had not yet clogged at the end of the 30 minute tow after having filtered 1,456 m³ (tow 33). These data indicate three possible explanations of the apparent superiority of silk in resistance to clogging; 1) silk mesh is "self-cleaning" at a higher rate, 2) the greater variability in sizes of silk apertures causes the clogging rate to be slower, or 3) the apertures in the silk mesh may be larger under tow than they are when examined under a miscroscope, thus making the comparison with nylon mesh inappropriate.

TABLE 4. Median performance values for all nets at all sites

Net number	R[1]	Mesh size (mm)	Mesh material	Net form	Initial efficiency percentage	San Pedro I[2] Volume (m³)	San Pedro I[2] Time min)	Catalina Volume (m³)	Catalina Time (min)	San Pedro II Volume (m³)	San Pedro II Time (min)
1	3·2	0·333	nylon	cone	92	47	2	112	2	–	–
2	4·8	0·333	nylon	cone	91	88	2	542	10	–	–
3	3·2	0·333	nylon	cylinder-cone	91	49	2	390	7	–	–
4	4·8	0·333	nylon	cylinder-cone	89[3]	123	3	1172	25	557	10
5	6·4	0·333	nylon	cylinder-cone	92	300	6	2564	50	–	–
6	4·8	0·571	nylon	cylinder-cone	94	71	2	3270	60	1137	20
7	3·2	0·550	silk	cylinder-cone	87[3]	194	4	3210	60	786	16
8	4·8	0·550	silk	cylinder-cone	93	320	7	3316	60	1461	30
9	4·8	0·450	silk	cylinder-cone	94	238	5	3069	60	961	18
10	1·6	0·333	nylon	cylinder	71	–	–	61	2	–	–
11[4]	3·2	0·333	nylon	cylinder	85	51	2	–	–	–	–
12	4·8	0·333	nylon	cylinder	92	103	3	2048	45	–	–
13	6·4	0·333	nylon	cylinder	93	383	9	3033	60	1194	20
14	6·4	0·201	nylon	cylinder	92	–	–	1554	28	654	12
15[5]	6·4	0·101	nylon	cylinder	92	–	–	1073	19	95	2
16	6·4	0·550	silk	cylinder	94	–	–	–	–	3294	60

[1] R is the ratio of filtering area to mouth area.

[2] Volumes and times are those filtered before trend of efficiency went below 85%.

[3] Used net.

[4] Net lost after one tow.

[5] Net torn by high filtration pressure.

SUMMARY OF RESULTS

The towing time and volume filtered before clogging for all 38 paired tows are listed in Table 3 with the mean tow velocity for each. In addition to the direct comparisons of nets mentioned above, we have collated the median results of all tows by form, mesh size, and mesh amount at the three towing sites in Table 4. We have omitted the comparison of mesh material for the reasons stated above.

Our predetermined performance requirement was that a net 1·0 m diameter at the mouth must filter 500 m³ at greater than 85% efficiency at 2·25 knots (116 cm/sec), to be acceptable for oblique survey tows. (This requirement represents a tow approximately 750 m long). By this standard, none of the nets was adequate for the turbid waters at San Pedro I. The 0·333 mm nylon mesh nets with an R of 3·2 were inadequate at all sites. All the other nets performed to standard in the Catalina tows (Table 4).

In the cylinder-cone nets of 0·333 mm mesh the volume filtered at more than 85% efficiency was increased six-fold by doubling the amount of mesh. This increase held at both the San Pedro I and Catalina sites. Figure 5 represents an attempt to estimate the amount of mesh necessary to sustain efficient filtration in waters like those at San Pedro I. The ordinate is the $\log_{10}$ of the volume filtered above 85% efficiency per square meter of mouth area and the abscissa is R. By extrapolation, an R of 7·8 would be necessary to filter 500 m³ efficiently through a 1 m diameter ring net at San Pedro I. Interpolation of the Catalina curve would lead one to predict that an R of 3·5 would have been adequate there.

DESIGN CRITERIA FOR PLANKTON NETS

It is not possible to specify design criteria for plankton nets without knowing the specific research problem for which the nets are to be used. A primary

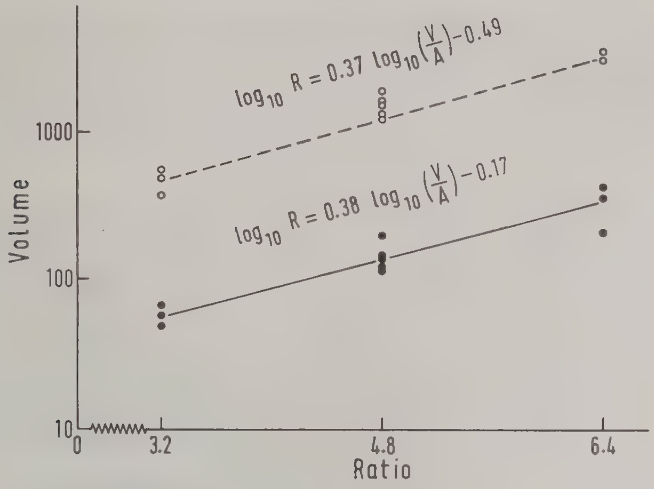


Figure 5. Sustained net performance and mesh amount. A comparison of the volume filtered per m^2 mouth area at greater than 85% efficiency at San Pedro I (solid dots) and Catalina (clear dots). (Net 3–3·2 times as much mesh aperture area as mouth area, tows 5, 6, 12, 20, 21, 27; net 4–4·8 times as much as mesh aperture area as mouth area, tows 1, 6, 8, 10, 11, 18, 19, 20, 28, 29; and, net 5–6·4 times as much mesh aperture area as mouth area, tows 11, 12, 13, 26, 27, 28). "Ratio" is the comparison of filtering area and mouth area; "Volume" is the logarithm of the cubic metres of water filtered per square metre of net mouth opening before clogging. The dashed line and the accompanying formula represent the median values of tows at the Catalina site (Secchi disc 24 m) and the solid line and the accompanying formula represent the median values for tows at the San Pedro I site.

design criterion for any quantitative plankton sampling net calls for sustained efficient filtration. Our results show that the most important design features in regard to sustained filtration efficiency are mesh size and filtering area. Changes in filtration efficiency during a tow affects the representation of the water column. It also affects the probability of capture of sensitive and motile organisms and the retention of the small and soft-bodied plankton.

It is necessary to have direct means of determining when significant clogging has occurred during a tow. We found that indirect means of judging whether clogging will take place, such as taking a Secchi disc reading, was not a suitable substitute for monitoring filtration efficiency. Inspection of the net after a tow was not reliable for determining whether it had clogged. After heavy clogging at San Pedro, the net was discolored but no indication of clogging appeared at the Catalina Island site, even when the net had been accepting less than half of the water presented to it at the end of the tow.

Ordinary flow meters (TSK or equivalent) mounted so that one is in the net mouth and one is isolated from the effects of the net and bridle, permit detection of significant clogging during the tow. If the flow rate can be telemetered to the ship, the instantaneous filtration efficiency can be obtained at any time during the tow as it was in this study.

This experiment was not extensive enough to define precisely the relation between mesh aperture size and clogging rate. This relation undoubtedly varies with changes in the size and species composition of the plankton. The best approximation that can be deduced from the present data is that clogging rate is roughly an inverse linear function of the individual mesh aperture area if all other net dimensions are constant. For example, the individual mesh aperture areas of 0·550 mm wide silk, 0·333 mm nylon, 0·201 mm nylon and 0·101 mm nylon are 0·30 mm^2, 0·11 mm^2, 0·04 mm^2 and 0·01 mm^2, respectively. At San Pedro II (Table 3) these nets filtered 3294, 1194, 654, and 95 m^3 before clogging.

One must determine carefully the minimum size of organism to be retained in designing a plankton net which will maintain high filtration efficiency over the entire course of the tow. SAVILLE (1959), in laboratory and field studies, demonstrated the size of silk mesh necessary for retention of fish eggs, fish larvae and crustaceans. It appears from his data that the maximum cross-sectional diameter of an organism must be greater than the diagonal of the mesh if it is to be retained. For the 0·550 mm silk and the 0·333 mm, 0·201 mm, and 0·101 mm nylon used in this study the diagonals are 0·78 mm, 0·47 mm, 0·28 mm and 0·14 mm respectively. Very few organisms having the same maximum cross-sectional diameter as the mesh *width* are retained.

One must have an estimate of the volume to be filtered and the clogging to be encountered before determining the ratio of filtering area to mouth area (R). Our tests show that the initial filtration efficiency is more than 85% whenever R is greater than 3·2. To this filtering area, which furnishes a high initial efficiency, must be added a reserve of mesh so that high efficiency can be maintained over the whole tow. To estimate the amount of reserve filtering area needed to sustain efficient filtration in conditions like those at San Pedro and Catalina, we have used the equations for the lines fitted in Figure 5, for 0·333 mm nylon mesh. For the "green" water at San Pedro the equation is:

$$\log_{10} R = 0{\cdot}38 \log_{10} \left(\frac{V}{A}\right) - 0{\cdot}17 \tag{5}$$

and for the "blue" water off Catalina Island the equation is:

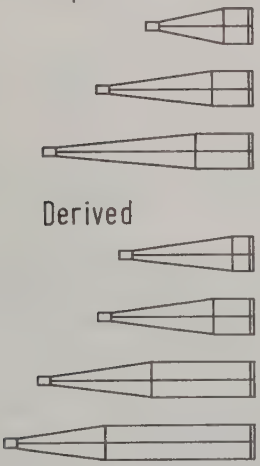
$$\log_{10} R = 0{\cdot}37 \log_{10} \left(\frac{V}{A}\right) - 0{\cdot}49 \tag{6}$$

Where

R = the ratio of filtering area to mouth area;
A = the mouth area of the net in m^2; and,
V = the volume to be filtered in m^3.

Nets of similar proportions should be useful in any mouth size; only the volumes to be filtered need to be changed. For instance, Figure 6 illustrates net designs with a mouth diameter of 1 m. To convert these designs to a 5-in. CLARKE-BUMPUS sampler, the designated volume must change according to the proportionate mouth areas. For example, the 500 m^3 volume through the 1 m diameter net is similar to 8 m^3 through a CLARKE-BUMPUS sampler.

We have found that the cylinder-cone net is preferable to either the cylinder or cone nets. The cylinder net was difficult to tow and recover. These tests show that all net forms had some degree of self-cleaning. The conical net was the least effective in this regard. We think that the cylindrical mesh has the greatest self-cleaning potential because it is aligned with the direction of the tow and is not subjected to the direct force of water impinging on the mesh as on any part of a cone. Furthermore, the mesh wall of the cylinder net oscillated. This oscillation induces a fluctuation of pressure across the mesh, which we



	R	Cubic metres Green water	Cubic metres Blue water
Experimental			
	3.2	49	390
	4.8	123	1172
	6.4	300	2564
Derived			
	3.5		500
	4.6		1000
	7.8	500	
	10.0	1000	

Figure 6. Net Design.

The upper section represents the proportions of the nets used in this study with 1 m diameter and 0·333 mm mesh size and the median values of the volume filtered at greater than 85% efficiency at the San Pedro I ("green water") and the Catalina ("blue water") towing sites. The lower section represents the interpolations and extrapolations of the "blue" and "green" formulas to provide ample filtering area in 1 m diameter nets to filter 500 m^3 and 1000 m^3 of water at greater than 85% efficiency at these towing sites. The derived net dimensions incorporate the recommendations of this paper that the conical section of the net contains an *R* of 3 and that the reserve filtering area be added in a forward cylinder.

believe to be responsible for the higher rate of self-cleaning. Since a net which is totally conical is inferior for sustained high filtration efficiency and a net which is totally cylindrical is unwieldy, we recommend design and use of a cylinder-cone net with a terminal conical section having an *R* of 3 and an anterior cylindrical section with enough reserve filtering area to sustain high filtration efficiency.

As an example of our approach to the design of a plankton net we describe the procedure by which we designed a net to sample the eggs of the northern anchovy (*Engraulis mordax*). The eggs are cylindrical with rounded ends with an average width of 0·65 mm. It was known that most of these eggs passed through or were extruded from the standard CalCOFI net whose mesh apertures have an opening 0·550 mm across and 0·78 mm on the diagonal. In operation, the new net was to be towed side by side with the standard net whose length of tow is fixed at about 14·5 minutes. The mesh size and *R* remained to be determined.

The mesh size of 0·333 mm was selected because the diagonal of 0·47 mm would retain anchovy eggs. It was decided that a mouth diameter of 0·5 m (0·2 m^2 mouth area) would obtain a sample containing a sufficient number of the eggs from 125 m^3 of water. Because some of the stations on each survey cruise are in inshore water where conditions are similar to those at San Pedro we decided to build the net with an R as determined by the "green" water formula (5):

$$\mathrm{Log}_{10} R = 0{\cdot}38 \log_{10}(125/0{\cdot}2) - 0{\cdot}17$$

The net constructed had 7·8 times as much filtering area as mouth area. The porosity of 0·333 mm monofilament Nitex* nylon is 0·46 thus the combined area of the mesh panels must total 3·39 m^2 ($0{\cdot}2 \times 7{\cdot}8/0{\cdot}46$). The terminal cone contained 1·30 m^2 of mesh ($0{\cdot}2 \times 3/0{\cdot}46$) and the remainder was added anteriorly as a cylinder. The terminal cone was truncate, 1·36 m long The reserve mesh area was a cylinder with a radius of 25 cm and a length of 1·33 m.

The filtration performance of this net has been checked for more than 2,000 tows on 11 monthly survey cruises of the CalCOFI in 1966. This net accepts 95% of the water presented to it in all the types of water found in the California Current at all seasons.

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Species Succession and Fishery Exploitation in the Great Lakes[1,2]

By Stanford H. Smith

U.S. Bureau of Commercial Fisheries
Ann Arbor, Michigan

ABSTRACT

The species composition of fish in the Great Lakes has undergone continual change since the earliest records. Some changes were caused by enrichment of the environment, but others primarily by an intensive and selective fishery for certain species. Major changes related to the fishery were less frequent before the late 1930's than in recent years and involved few species. Lake sturgeon (*Acipenser fulvescens*) were overexploited knowingly during the late 1800's because they interfered with fishing for preferred species; sturgeon were greatly reduced in all lakes by the early 1900's. Heavy exploitation accompanied sharp declines of lake herring (*Leucichthys artedi*) in Lake Erie during the 1920's and lake whitefish (*Coregonus clupeaformis*) in Lake Huron during the 1930's. A rapid succession of fish species in Lakes Huron, Michigan, and Superior that started about 1940 has been caused by selective predation by the sea lamprey (*Petromyzon marinus*) on native predatory species, and the resultant shifting emphasis of the fishery and species interaction as various species declined. Lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), the deep-water predators, were depleted first; this favored their prey, the chubs (*Leucichthys* spp.). The seven species of chubs were influenced differently according to differences in size. Fishing emphasis and predation by sea lampreys were selective for the largest species of chubs as lake trout and burbot declined. A single slow-growing chub, the bloater, was favored and increased, but as the large chubs declined the bloater was exploited by a new trawl fishery. The growth rate and size of the bloater increased, making it more vulnerable to conventional gillnet fishery and lamprey predation. This situation in Lakes Michigan and Huron favored the small alewife (*Alosa pseudoharengus*) which had recently become established in the upper Great Lakes, and the alewife increased rapidly and dominated the fish stocks of the lakes. The successive collapses of various stocks after periods of stable production may give some indication of their sustainable yield. The sea lamprey is being brought under control in Lakes Superior, Michigan, and Huron; lake trout are being established; and chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), kokanee salmon (*O. nerka*), and the splake, a hybrid of lake trout and brook trout (*Salvelinus fontinalis*), are being introduced to reestablish a new species balance. Fish stocks are in a state of extreme instability in these lakes. Careful control of stocking programs and fisheries, and coordination of management among the various states of the United States and the province of Canada (Ontario) which manage the fish stocks, will be required to restore and maintain a useful fishery balance.

INTRODUCTION

It was not apparent until recent years that the intensive and selective fishery of the Great Lakes over the past century has been a significant factor in a major modification of fish stocks. A succession of fish species would be expected during the natural aging process of the Great Lakes, but recent progressive

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changes in species composition have been rapid and obviously accelerated by influences of man, both by enrichment of the environment with wastes and by despoilment of the most abundant or preferred species of fish.

The species composition of fish in the Great Lakes has undergone continual change since the earliest records (Smith and Snell, 1891) but never have changes been more rapid or more drastic than in recent years. Environmental changes in Lake Erie (Beeton, 1961) and the related changes in the composition of the fish population and other aquatic organisms (Smith, 1962) have received considerable publicity in recent years. Modifications of fish stocks in the upper Great Lakes (Superior, Michigan, and Huron), which are deeper and more oligothophic, have been equal to or greater than changes in Lake Erie, but appear not closely related to modification of the physical–chemical environment. Although the water quality of the upper Great Lakes has undergone some changes (Beeton, 1965), these have not been the primary cause of what appears, with few exceptions, to be an irreversible succession of the major fish species. Recent changes have led to a state of biological instability in the mid-1960's that is almost unparalleled in the history of fishery science.

EARLY CHANGES

Since its beginning over a century ago the fishery of the Great Lakes has always shown preference for species that were abundant and in high demand. Less than a dozen species have been major contributors to the catch and, despite an intensive selective fishery, major changes in these species were few and local until recent years. Those that were influenced greatly by the fishery before the late 1930's were the lake sturgeon (*Acipenser fulvescens*), lake herring (*Leucichthys artedi*[3]), and lake whitefish (*Coregonus clupeaformis*).

Lake Sturgeon

The lake sturgeon was the first species affected by intensive exploitation and the only one that was knowingly depleted by man. Although the commercial value of the sturgeon was not great, they were abundant in all of the Great Lakes before 1900, particularly near shore where fishing for other species was heavy. These large fish frequently damaged gear fished for more valuable species, and were fished heavily to remove them from the fishing grounds (Harkness and Dymond, 1961). The recorded catches of sturgeon in the late 1800's exceeded 1 million lb annually in each of Lakes Michigan, Huron, and Erie, and often reached several hundred thousand pounds in Lakes Ontario and Superior (Baldwin and Saalfeld, 1962). The recorded catches represent an unknown fraction of the total poundage taken; many were killed and thrown back in the lake or left to rot on the beaches. As a consequence of their slow growth and late maturity the accumulated stocks of adult fish were soon reduced to insignificance and became so scarce by the 1920's that sturgeon fishing was prohibited throughout most U.S. waters of Lakes Superior, Michigan, and Huron. Restrictions have been lifted in the State of Michigan waters of these lakes in recent years to permit the fishermen to keep sturgeon which are caught incidental to other fishing. The total production, however, is only a few thousand pounds in any of the lakes.

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[3] Some authors include *Leucichthys* (ciscoes) in the genus *Coregonus* (whitefishes). I prefer the separate genera for clarity, and because a recent acrylamide electrophoretic study of blood serum made by Richard Chellevold at the University of Michigan showed that the serum proteins distinctly separate ciscoes and whitefishes of both North America and Europe; that ciscoes and whitefishes each produce identical electrophoretic patterns between the continents; and that differences between ciscoes and whitefishes of Europe are the same as the differences in North America. Thus it is evident that the two groups are genetically distinct; have had separate origins; have attained their circumpolar distribution independently; and deserve generic distinction.

Partial protection of the sturgeon did not seem to increase its abundance noticeably, nor has an incidental fishery seemed to cause a decline. The only noticeable recent decline has been in Lake Erie, where catches have reached new lows since the mid-1950's, which may reflect recent unfavorable changes in the environment (Carr, 1962; Carr and Hiltunen, 1965; Carr et al., 1965). The lake sturgeon undoubtedly will continue to live in the Great Lakes at low abundance until influenced adversely by the changing environment, or by a fishery for another species that raises the incidental catch above the limit of its biological yield.

Lake Herring

The collapse of the lake herring population in Lake Erie in the mid-1920's (Van Oosten, 1930) was the first precipitous change in the fish stocks of the Great Lakes. Historically the lake herring has been very abundant and the most productive species in the Great Lakes — frequently contributing one-third to one-half of the catch of various lakes. In Lake Erie, lake herring were particularly abundant and were larger than in the other lakes. Because of these factors and the proximity of markets in large eastern cities, the fishery was intense. Before the collapse of the population the recorded catches were usually greater than 20 million lb annually and ranged as high as 49 million lb. Actual catches were much greater, however, as large quantities were frequently discarded during periods when catches were heavy and the market was glutted (Van Oosten, 1930).

The cause of the collapse of lake herring stocks in Lake Erie was never settled because detailed biological, ecological, and fishing data were lacking, but there are two pertinent factors that can be considered in retrospect. Fishing was very intense in the years preceding the decline and was particularly intense in the fall of 1924 — the year before the decline — due to an unusual concentration of lake herring in the east end of the lake (Van Oosten, 1930). After initial collapse the lake herring produced only one strong year-class — that hatched in 1944 (Scott, 1951) — although substantial spawning stocks were present until the mid-1950's. If the fishing rate before the decline was near that required for full utilization of the biological potential of the stock, and if recruitment was lowered due to reduction of spawning stocks or to environmental variability in the early 1920's, the catch would have exceeded the maximum sustainable yield. This relation must lead to a swift decline in the stock (Ricker, 1963).

Although intensive exploitation and possible interaction with environmental change may have caused the sharp drop in lake herring stocks in the 1920's, a subsequent decline since the mid-1940's to extreme rarity approaching extinction in the mid-1960's undoubtedly is a response to increasingly unfavorable physical–chemical or biological environmental conditions. Fish collected in 1957 showed average 1st-year growth of lake herring of only 2.7 inches (Scott and Smith, 1962) which is much below the calculated 1st-year growth for lake herring in Lake Superior (4.7 inches; Dryer and Beil, 1964), Green Bay, Michigan (5.2 inches; Smith, 1956), or Saginaw Bay, Lake Huron (6.0 inches; Van Oosten, 1929). The slowest 1st-year growth recorded for the lake herring of 11 other lakes in the Great Lakes region was 3.4 inches (Carlander, 1953). Fish of Lake Erie, however, have been noted for their rapid growth. Examination of scales from Lake Erie lake herring showed that the average 1st-year growth was 7.2 inches — the highest value recorded for this species — for fish collected in 1945. The decline to 2.7 inches in 1957 provides strong evidence that the recent reduction of the lake herring in Lake Erie is more likely a result of environmental stress than a result of the small catches that have continued, and which have been mostly incidental to fishing for other species.

Lake Whitefish

The second collapse of a local fishery during the early period involved the development of a new type of gear — the deep trap net — that was very efficient for capture of lake whitefish in Lake Huron (Van Oosten et al., 1946). These nets were introduced in Lake Huron in 1928 at a time when whitefish abundance was high and apparently increasing. Beginning in 1930 their use expanded rapidly throughout the U.S. waters of the lake (this gear was never permitted in Canada), and the net proved particularly effective in central and southern Lake Huron. Over 4.1 million lb of whitefish were taken from the lake in 1931. As the nets were moved successively into various sections of the lake, local stocks were depleted rapidly. Thus, although stocks in different locations declined sharply, the total production of the lake did not decrease abruptly. The catch had declined to 1.9 million lb in 1935 when restrictions were imposed that prohibited setting trap nets in water deeper than 80 ft, but continued to decline to less than 0.1 million lb in 1942. Predation by the sea lamprey (*Petromyzon marinus*) discussed later may have been responsible in part for this low. Except for progeny of a very successful 1943 year-class that resulted in catches of about 3 million lb in U.S. waters in 1947 and 1948, the catch of lake whitefish has been less than 0.2 million lb in most years after the 1942 low (Baldwin and Saalfeld, 1962). A high mortality of the 1943 year-class and the recent low have been attributed to sea lamprey depredations rather than depletion through overfishing (Hile and Buettner, 1959).

OTHER SPECIES

Although unrelated to exploitation, collapse of another fish stock which took place in early 1940's should be mentioned briefly. The American smelt (*Osmerus mordax*) was endemic in Lake Ontario but was introduced into the Lake Michigan drainage in 1912 and underwent a population explosion in Lakes Michigan and Huron in the 1930's (Van Oosten, 1937). The smelt population suffered a severe mortality during the fall and winter of 1942–43 probably due to a bacterial or virus disease (Van Oosten, 1947). The commercial production in Lake Michigan, where a thriving fishery for smelt had been established, fell from 4.8 million lb in 1941 to 4500 lb in 1944. The population recovered, however, and contributed to a very productive fishery as it became established in all of the lakes above Lake Ontario. The fishery was particularly productive in Lake Michigan where the catch reached a maximum of 9.1 million lb in 1958, and in Lake Erie where a peak catch of 19.2 million lb was produced in 1962.

A selective fishery for the larger chubs or deepwater ciscoes (*Leucichthys* spp.) influenced the species composition of this closely related group of species during the late 1800's and early 1900's. The early stages of these changes could not be measured because the various species of chubs were taken in the same net and were so similar that they were not sorted by the fishermen or listed separately in the catch statistics. But early records indicate clearly that the two largest species (*L. nigripinnis* and *L. johannae*) did, in fact, decline (Hile and Buettner, 1955). This early decline of certain species of chubs is discussed later in relation to the extreme modification of the chub population in recent years.

RECENT CHANGES

A rapid sequence of catastrophic changes which started in the 1940's led to a major alteration of the fish stocks in the Great Lakes. Until the 1940's the fishery of the Great Lakes as a whole was stable and productive despite loss of the sturgeon and the collapse of a few stocks in certain lakes. All preferred species continued in abundance somewhere in the Great Lakes; although many showed varying degrees of cyclical fluctuation, the composition of the total catch showed no marked changes or trends. The total production had stabilized and fluctuated only slightly around 100 million lb after declining from highs which often exceeded 140 million lb before 1920.

The major events that started in the 1940's involved the upper three lakes (Huron, Michigan, and Superior). The resulting succession of species resembled similar changes that apparently had taken place earlier in Lake Ontario, but which had gone almost unnoticed because the fishery was small and little studied. Changes that were progressing in Lake Erie, and which have accelerated since the 1940's, are not discussed here because both selective exploitation and environmental change were involved and their interactions are not understood.

The most intensive studies in the upper three lakes were made in Lake Michigan which is used here to illustrate similar events in Lakes Huron and Superior. The primary differences among these lakes have been timing and degree — in general, changes in Lake Huron started earlier and appear to have progressed further than Lake Michigan, and in Lake Superior they started later and have not advanced as far. The ultimate outcome may differ among the three lakes — their limnological characteristics differ somewhat, all are undergoing rapid change, and varying types and degrees of management are being imposed when each lake is at a different stage of change.

The Lake Michigan Fishery

The history of fishery exploitation in Lake Michigan was typical of the other Great Lakes. The highest annual production occurred near or before the turn of the century when the fishery had become well established. The catch exceeded 40 million lb in 4 of the 13 years for which statistics were available between 1897 and 1909 (Baldwin and Saalfeld, 1962), and averaged 35 million lb (Table I). In subsequent periods the total catch showed no marked variations or trends (Fig. 1) and averaged about 25 million lb until 1966 when the catch increased sharply to over 42 million lb due primarily to a greater catch of alewives. Nine species have been major contributors to the catch; they have constituted 95.6–99.8% of the catch in periods for which records of all species are complete (Table I).

At the turn of the century seven major species were represented in the catch (Table I). The lake trout (*Salvelinus namaycush*) and lake herring were the largest contributors, and the carp (*Cyprinus carpio*), which was introduced into the lake in the late 1800's, constituted less than 1% of the catch. Despite increased abundance of carp and the subsequent introduction and establishment of the smelt, the relative contribution of the native species to the catch showed no marked changes or trends until the 1945–49 period when the lake trout catch declined sharply. Subsequent species changes took place in swift succession (Fig. 1). In 1966, the catch was dominated by the alewife (*Alosa pseudoharengus*) which invaded the lake in the late 1940's (first recorded in 1949; Miller, 1957); exotic species constituted nearly 77% of the catch; and the portion of the catch composed of lake trout, lake herring, suckers (*Catostomus* spp. and *Moxostoma* spp.), and whitefish was only 4.4% as compared with more than 82% in the 1898–1909 period.

Several factors contributed to this extreme change. Much is known about these factors and their interactions although the exact mechanisms that brought about the change are incompletely understood. Unquestionably, predation of the sea lamprey initiated the events that led to the extreme decline of the lake trout in the upper Great Lakes. The resultant pressures of a shifting fishery and a population explosion of the alewife were factors of major significance. How these factors operated is illustrated by examining the changes in the deepwater stocks — lake trout and chubs — which occupy the area most strongly affected by sea lamprey predation, and the changes in the fishery.

TABLE I. Catch of major species and total commercial catch (thousands of pounds) per year in Lake Michigan for various periods.

	Native species						New species			Total major species			
Period	Lake trout	Lake herring	Suckers	Whitefish	Chubs	Yellow perch	Carp[a]	Smelt[b]	Alewife[c]	Pounds	Percentage of total catch	Other species	Total catch
1898–1909	7,225	16,977	1,810	2,715	2,061	3,866	261	–	–	34,915	–	–[d]	35,149
1910–1919	6,763	8,642	4,035	1,670	3,525	2,411	247	–	–	27,293	–	–[d]	27,059
1920–1929	7,001	4,015	2,117	2,111	2,902	1,537	679	–	–	20,362	–	–[d]	20,477
1930–1934	5,342	4,985	2,258	3,730	4,387	1,199	769	425	–	23,075	98.0	465	23,540
1935–1939	5,038	4,621	2,280	1,201	5,295	2,406	1,605	1,462	–	23,908	98.7	312	24,220
1940–1944	6,579	1,830	2,125	1,351	1,971	2,729	1,702	2,913	–	21,200	97,8	474	21,674
1945–1949	2,675	6,044	1,901	3,756	5,435	1,446	1,319	765	–	23,324	95.6	1,066	24,407
1950–1954	14	8,000	882	1,436	10,482	1,963	1,170	4,384	–	28,334	97.1	848	29,182
1955–1959	<1	3,639	652	105	9,947	3,055	1,785	6,983	568	26,735	97.8	592	27,327
1960	<1	233	767	124	12,695	3,285	1,416	3,267	2,370	24,158	99.4	153	24,311
1961	<1	177	494	412	12,133	4,959	1,842	2,152	3,199	25,370	99.3	189	25,559
1962	<1	116	263	278	11,115	4,050	1,206	1,546	4,742	23,317	99.3	158	23,475
1963	<1	41	299	298	7,460	4,872	1,277	1,203	5,396	20,795	98.9	226	21,021
1964	<1	34	215	788	5,172	5,835	1,320	969	11,744	26,080	99.5	121	26,201
1965	<1	47	168	995	7,441	1,297	2,016	927	14,007	26,900	99.7	94	26,994
1966	<1	49	402	1,422	7,228	654	2,713	1,110	29,002	42,580	99.8	97	42,677

[a] Introduced in the late 1800's.
[b] Introduced into Crystal Lake tributary to Lake Michigan in 1912.
[c] Invaded the upper Great Lakes via the Welland Canal and was first reported in Lake Michigan in 1949.
[d] Data incomplete.

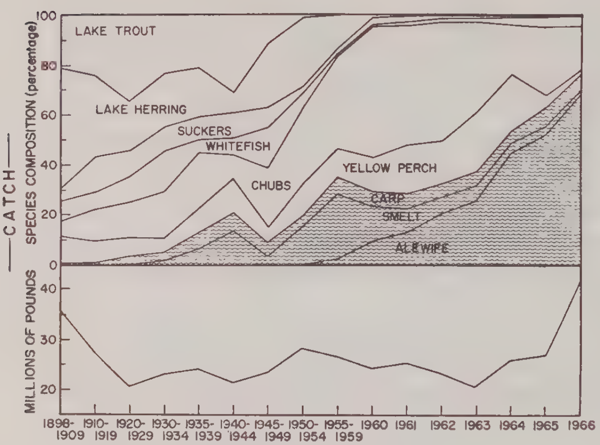


FIG. 1. Contribution of major species (percentage) and total commercial catch (pounds) of Lake Michigan for various periods 1898–1966. Shaded portion indicates exotic species.

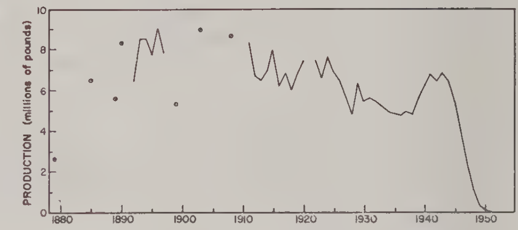


FIG. 2. Commercial production of lake trout in Lake Michigan for years of records 1879–1955.

DECLINE OF THE LAKE TROUT

The lake trout has provided the most stable fishery of the Great Lakes. It was particularly productive in Lakes Superior, Huron, and Michigan, where catches usually exceeded 4, 5, and 6 million lb, respectively, and had not fluctuated widely before the declines in recent years. Biological information about the early stocks is not available. It is possible, however, as Kennedy (1954) has observed for lake trout stocks in Great Slave Lake, that recruitment was not strongly cyclic and that annual fluctuations of year-class strength were not great.

Lake trout production has been highest in Lake Michigan but the history of the catch was similar for all three lakes even though timing differed somewhat (Hile, 1949; Hile et al., 1951a, b). Catches in Lake Michigan increased in 1879–90 during the development of the fishery on the newly exploited stocks (Fig. 2). Production was highest during 1890–1911 and was characterized by periods of relative stability in 1912–26 and 1927–39 at slightly lower levels (Hile et al., 1951a). The catch increased briefly in 1940–44, after which it underwent the collapse attributed to sea lamprey predation, and neared extinction by the mid-1950's due to a complete failure of natural reproduction after 1948 (Eschmeyer, 1957).

The collapse of the lake trout populations in the upper Great Lakes stimulated a massive effort to control the sea lamprey (Moffett, 1958). The early research has produced information on sea lamprey abundance during its population explosion that helps to interpret the relation between sea lamprey predation and lake trout decline, and the subsequent upset of the chub stocks. Although the measures of sea lamprey abundance over the longest period for each lake are based on spawning adults entering only one or a few streams (Table II), their agreement with trends in counts available for shorter

TABLE II. Number of sea lampreys counted during spawning runs in various streams in Lakes Huron, Michigan, and Superior, and their abundance index expressed as percentage of the average for the period of counts in each lake.[a]

	Lake Huron[b]		Lake Michigan[c]			Lake Superior[c]	
Year	Ocqueoc River	Abundance	Hibbards Creek	Three[d] streams	Abundance	Five[e] streams	Abundance
1944	4,488	50	–	–	–	–	–
1945	6,144	68	–	–	–	–	–
1946	8,072[f]	90	125	–	3	–	–
1947	10,000	111	596	–	16	–	–
1948	13,000	145	989	–	27	–	–
1949	24,634	275	1,579	–	43	–	–
1950	18,822	210	5,431	–	148	–	–
1951	19,393	216	12,640	–	345	–	–
1952	9,437	105	3,302	–	90	–	–
1953	11,676	130	9,247	–	252	1,424	24
1954	10,183	113	7,279	–	199	2,614	45
1955	13,683	153	6,395	18,279	164	3,096	53
1956	10,923[f]	122	5,325	19,653	155	8,048	138
1957	8,163	91	6,525	18,175	165	12,983	223
1958	5,465[f]	61	2,563	10,669	80	6,649	114
1959	2,766	31	2,330	8,636	68	8,224	141
1960	7,560	84	–	6,651	52	12,897	221
1961	4,715	53	–	12,886	101	13,305	228
1962	5,205	58	–	8,089	63	2,743	47
1963	4,674	52	–	7,461	59	3,838	66
1964	2,677	30	–	4,593	36	2,250	39
1965	1,390	15	–	3,277	26	2,205	38
1966	3,273	36	–	1,168	9	1,359	23

[a] The abundance for Lake Michigan was obtained by adjusting the total catch of the three streams to equal the catch of Hibbards Creek for the period of overlap (1955–59), averaging the figures for each year during this period, and extending the series based on the 1959 average and the percentage change from year to year for counts of the three streams.

[b] Records supplied by Dr Vernon C. Applegate.

[c] From reports of the Great Lakes Fishery Committee, and meeting reports and annual reports of the Great Lakes Fishery Commission available at the library of the Ann Arbor Laboratory, U.S. Bureau of Commercial Fisheries.

[d] Bark, Cedar, and Sturgeon rivers.

[e] Betsy River, Furnace Creek, Miners River, Sucker River, and Two Hearted River.

[f] No counts made; estimates are means of preceding and following years.

periods for other streams at various times suggests that these measures reflect closely the trends of abundance for each of the lakes.

The abundance of sea lampreys was very low in all three of the upper Great Lakes at the time when lake trout stocks started to decline (Fig. 3). The lake trout were unquestionably the prime prey of the sea lamprey as lake trout were the only abundant species of large fish that inhabited the colder (subthermocline) regions of the lakes preferred by the sea lamprey. Although large burbot (*Lota lota*), which occupied this area were less abundant and suffered the same fate as the lake trout, it can be safely assumed that the trout suffered the brunt of the earliest predation. This predation could not have been great since spawning runs into the larger streams reportedly amounted to less than a hundred individuals before and during the early stages of lake trout decline (Vernon C. Applegate, personal communication).

The decline of lake trout in Lake Michigan was particularly abrupt, however, and may reflect the possible combined effect of increased predation by sea lampreys that were able to move freely from Lake Huron into Lake Michigan, and by the greater exploitation of lake trout by the commercial fishery in the period just before the decline. The increased catch occurred during the period when lake trout stocks were declining in Lake Huron and may be related in part to greater demand and higher prices at the time. Although the greater production may have been due in part to improvement in stocks since it was not accompanied by increased fishing effort in State of Michigan waters (Hile et al., 1951a), the higher production resulted mostly from the increased catch in Illinois which rose from 259 to 972 thousand lb (275% increase) between the periods 1927–39 and 1940–44. The Illinois catch had never been large and the increased catch of 713 thousand lb must have resulted in part from greater fishing intensity because of proximity to the Chicago market, the strong demand during World War II, and the declining catch in Lake Huron. It is also unlikely that the abundance increased to this degree in Illinois waters alone as sharp fluctuations in abundance were not characteristic of the lake trout and lake trout move freely throughout the lake (Smith and Van Oosten, 1940). This increase alone was more than 13% above the 1927–39 average for Lake Michigan, and if only half of it were attributed to greater fishing effort, it could have initiated a weakening of the lake trout stocks.

If fishing had been near the optimum rate in earlier years, only a small increase in exploitation would have been necessary to start a decline in the stocks. In an example based on biological characteristics similar to those of lake trout, Ricker (1963) determined that a 14% increase in exploitation separated maximum yield and no yield (collapse of the stock), and that half this increase (7%) would initiate a sharp decline. Thus, an increase of only 370–740 thousand lb over the average of about 5.3 million lb for the earlier period of stability during 1927–39 (Hile et al., 1951a) may have been sufficient to initiate the decline of the lake trout stock, which then became weakened further by sea lamprey predation.

INTERACTION OF THE DEEPWATER FISHERIES

Until the establishment of the alewife in recent years, lake trout and chubs were the only species that were abundant in the deepwater area of Lake Michigan and important in the fishery. Although the interactions between the lake trout and chub fisheries were complex (Hile and Buettner, 1955), the two fisheries were essentially alternate; they usually employed the same boats and fished in much the same areas, but differed in the use of large-mesh gillnets for lake trout and small mesh for chubs.

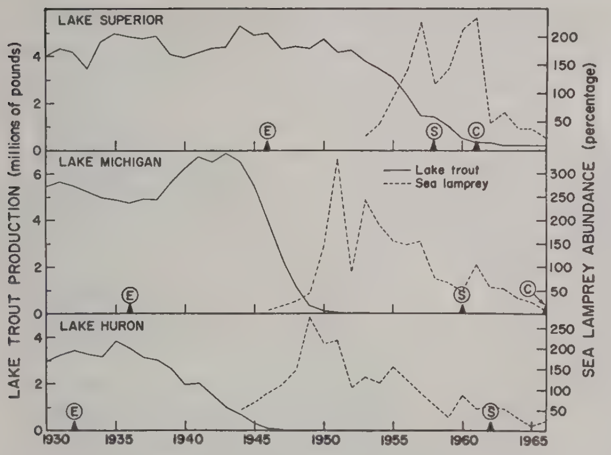


FIG. 3. Production of lake trout and abundance of the sea lamprey in Lakes Superior, Michigan, and Huron, and the time of first sea lamprey record or establishment (E), initiation of chemical control (S), and completion of the initial series of chemical treatment (C) in each Lake.

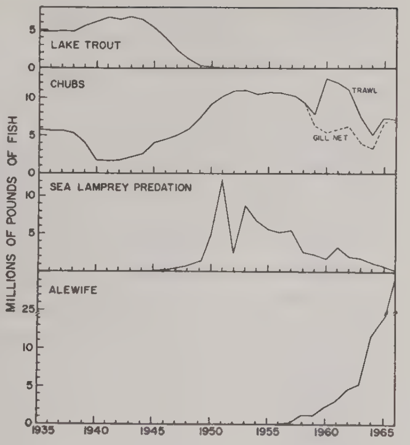


FIG. 4. Production of lake trout, chubs, and alewives, and the estimated pounds of fish destroyed by sea lampreys of the spawning population of Lake Michigan.

The chub fishery was depressed by reduced effort during the war years in 1940–44, but recovered as the lake trout declined; the change reflected a transfer of effort from lake trout to chubs (Hile and Buettner, 1955). The chub catch reached a record high of 7 million lb in 1949 and increased to a high period of production above 10 million lb during 1951–57 (Table III). It was during these same peak years of chub production that the sea lamprey attained its greatest abundance. Because the deep waters contained no other prey (lake trout and burbot had both disappeared) the chubs received the impact of sea lamprey predation (Moffett, 1957). The estimated pounds of fish killed by the number of sea lampreys that had survived to spawn exceeded 11 million lb in 1951 and was above 5 million lb until 1957 except for a low of 3 million lb in 1952. These estimates are conservative because they are based on counts of spawning-run sea lampreys and do not account for an unknown amount of predation by lampreys that did not survive to spawn.

The consequence of this extreme pressure of high commercial production and sea lamprey predation on the chub population was severe. Of the seven species of chubs that inhabited Lake Michigan the two largest (*Leucichthys johannae* and *L. nigripinnis*) had become extinct, and the four species of intermediate size (*L. alpenae*, *L. kiyi*, *L. reighardi*, and *L. zenithicus*) had been seriously depleted as shown in a survey during 1960–61 (Smith, 1964). The smallest and slowest growing chub, the bloater (*L. hoyi*), was favored during this period and became very abundant. It had been a primary food of the lake trout (Van Oosten and Deason, 1938) and most were too small to be taken profitably in commercial gillnets or serve as suitable prey for the sea lamprey. As the supply of larger chubs declined during the late 1950's, the commercial gillnet catch declined, and the abundance of sea lampreys

TABLE III. Production of lake trout, chubs, and alewives, and estimated pounds of fish destroyed by spawning run sea lampreys in Lake Michigan in 1935–66.

Year	Lake trout	Chubs			Alewife	Fish destroyed by sea lamprey[a]
		Gillnet	Trawl	Total		
		(Thousands of pounds of fish)				
1935	4,873	5,794	–	5,794	–	–
1936	4,763	5,674	–	5,674	–	–
1937	4,988	5,579	–	5,579	–	–
1938	4,906	5,404	–	5,404	–	–
1939	5,660	4,025	–	4,025	–	–
1940	6,266	1,648	–	1,648	–	–
1941	6,787	1,630	–	1,630	–	–
1942	6,484	1,755	–	1,755	–	–
1943	6,860	2,214	–	2,214	–	–
1944	6,498	2,607	–	2,607	–	–
1945	5,437	4,221	–	4,221	–	–
1946	3,974	4,525	–	4,525	–	116
1947	2,425	5,087	–	5,087	–	554
1948	1,197	5,929	–	5,929	–	919
1949	342	7,421	–	7,421	–	1,467
1950	54	9,291	–	9,291	–	5,046
1951	11	10,301	–	10,301	–	11,744
1952	4	11,098	–	11,098	–	3,068
1953	[b]	11,151	–	11,151	–	8,591
1954	[b]	10,568	–	10,568	–	6,762
1955	[b]	10,895	–	10,895	–	5,576
1956	0	10,913	–	10,913	[b]	5,275
1957	0	10,546	–	10,546	220	5,622
1958	0	9,583	–	9,583	1,357	2,711
1959	[b]	6,392	1,404	7,796	1,264	2,313
1960	[b]	5,530	7,129	12,695	2,370	1,782
1961	[b]	5,915	6,218	12,133	3,199	3,452
1962	[b]	6,346	4,769	11,115	4,742	2,167
1963	26	4,050	3,410	7,460	5,396	1,999
1964	[b]	3,381	1,791	5,172	11,744	1,230
1965	[b]	6,857	583	7,440	14,007	877
1966	[b]	6,990	238	7,228	29,002	313

[a] Based upon a proportional expansion of the abundance index (Table II) to reflect the sea lamprey count in 1958 when the maximum number of streams were blocked with counting barriers (Great Lakes Fishery Commission, 1958) which was doubled on the assumption that one-half of the spawning streams were blocked, and that each lamprey killed 37 lb of fish to reach maturity (Packer and Lennon, 1956).

[b] Less than 500 lb. Most lake trout caught since 1953 were hatchery-reared fish planted to measure survival and planting techniques.

and their predation decreased (Fig. 4), but the total chub catch increased to a new high of 12.7 million lb in 1960 (Table III). This increase resulted from the use of trawls which had not been employed in the Great Lakes fishery until they were introduced in the late 1950's to catch the small bloater which had become very abundant by the mid-1950's (Moffett, 1957) and alewives which were starting to become abundant.

Most of the bloaters and the alewife were too small for the human food market, and trawling provided an efficient means of catching them in large quantity at low cost for animal food and fish meal. Markets for alewives were not well established, however, and the population had not increased sufficiently to support heavy production during all seasons. The trawl fishery was restricted to certain species and depths of fishing so that the only abundant species that could be taken by trawling were alewives and chubs. Thus, during the early stages of the trawl fishery bloaters composed the greater part of the catch (Table III) because they were very abundant, available during all seasons, brought a higher price than alewives on the animal-food market, and included some large chubs (about 7% of the catch) that brought a high price on the human-food market.

Even the gillnet fishery became dependent on bloaters when species of large chubs had become scarce during the late 1950's. The human-food market accepted smaller chubs at lower price, but the bloaters were also becoming larger (Tables IV and V). The average length of bloaters in both southern

TABLE IV. Length distribution (percentage) of bloaters taken in trawls in southern Lake Michigan at Grand Haven (1954, 1960) and Saugatuck (1962–66).

Length (*inches*)	Year						
	1954	1960	1962	1963	1964	1965	1966
2.5–2.9	0.1	–	–	–	–	–	–
3.0–3.4	0.1	–	–	–	–	–	–
3.5–3.9	0.5	–	–	–	–	–	–
4.0–4.4	1.2	T	T	–	T	–	–
4.5–4.9	1.3	T	0.2	–	T	–	0.1
5.0–5.4	1.2	0.1	T	T	–	T	0.3
5.5–5.9	10.8	0.2	0.1	0.1	T	–	0.1
6.0–6.4	22.5	0.8	–	0.1	T	0.1	0.1
6.5–6.9	23.8	3.0	0.6	0.2	0.1	0.1	0.1
7.0–7.4	12.7	20.1	9.2	3.3	3.6	2.0	0.9
7.5–7.9	10.3	32.3	35.0	26.4	25.6	17.7	10.1
8.0–8.4	6.4	19.9	28.4	34.6	32.6	28.4	23.8
8.5–8.9	4.9	11.5	13.8	17.2	19.2	22.9	26.3
9.0–9.4	2.4	7.3	6.8	10.0	10.4	15.9	20.3
9.5–9.9	1.2	3.4	3.8	4.9	5.7	7.5	10.7
10.0–10.4	0.5	1.1	1.6	2.3	1.9	3.7	5.1
10.5–10.9	0.1	0.2	0.4	0.7	0.6	1.3	1.5
11.0–11.4	–	0.1	0.1	0.2	0.2	0.3	0.5
11.5–11.9	–	–	–	–	0.1	0.1	0.1
12.0–12.4	–	–	–	–	–	T	–
Avg length:	6.86	7.98	8.15	8.36	8.38	8.59	8.78
No. of fish:	4,336	16,454	1,745	5,215	8,720	3,055	1,771
Percentage >9.0 inches:	4.2	12.1	12.7	18.1	18.9	28.8	38.2

TABLE V. Length distribution (percentage) of bloaters taken in trawls at Manistique in northern Lake Michigan in various years between 1955 and 1964.

Length (*inches*)	1955	1961	1964
5.0–5.4	0.8	–	–
5.5–5.9	0.3	–	–
6.0–6.4	1.3	0.1	–
6.5–6.9	1.8	–	–
7.0–7.4	6.7	2.8	0.4
7.5–7.9	13.2	11.5	1.9
8.0–8.4	26.9	28.7	9.9
8.5–8.9	24.0	24.3	20.8
9.0–9.4	12.4	17.0	29.5
9.5–9.9	7.7	10.2	18.7
10.0–10.4	2.8	3.7	11.2
10.5–10.9	1.5	1.3	5.1
11.0–11.4	0.3	0.2	1.7
11.5–11.9	0.3	0.2	0.6
12.0–12.4	–	–	0.2
Avg length:	8.46	8.68	9.30
No. of fish:	387	1635	475
Percentage >9.0 inches:	25.0	32.6	67.0

and northern Lake Michigan increased in every year for which data are available between 1954 and 1966. The mean length in southern Lake Michigan increased almost 2 inches during this period, and the percentage of bloaters large enough for the human-food market (usually >9 inches) increased from 4.2 to 38.2%. In northern Lake Michigan the length increased about 1 inch between 1955 and 1964, and the bloaters suited for human food rose from 25.0 to 67.0%. Since the average length of bloaters taken in 1960–61 increased from south to north (Table VI), it might be assumed that the length increased throughout the lake during the period of 1954–66. Preliminary studies show that this increase in average length reflects both an increase in average age and an increase in growth rate.

The combined influence of the new trawl fishery and the increase in size of bloaters which made them better suited for the gillnet fishery resulted in the largest chub catches of record in Lake Michigan in 1960–62. Sea lamprey predation of about 2 million lb or more during this period was also directed primarily at bloaters, many of which had increased to a size more vulnerable to lamprey predation.

The chub fishery declined sharply after this period of record catch (Fig. 4). Deaths from botulism in October 1963 of several persons who had eaten smoked chubs from the Great Lakes undoubtedly contributed to the low catches in 1963–64, but the catch through September 1963 had already declined

TABLE VI. Length distribution (percentage) of bloaters taken in trawls at various ports in Lake Michigan in 1960 and 1961.

Length (*inches*)	St. Joseph 1960	Milwaukee 1960	Grand Haven 1960	Frankfort 1961	Sturgeon Bay 1961	Charlevoix 1961	Manistique 1961
2.5–2.9	–	–	–	0.1	–	–	–
3.5–3.9	0.1	–	–	–	–	–	–
4.0–4.4	–	–	T	–	–	–	–
4.5–4.9	–	0.1	T	0.1	–	–	–
5.0–5.4	T	T	0.1	0.5	–	–	–
5.5–5.9	0.1	0.1	0.2	0.5	–	–	–
6.0–6.5	0.4	1.0	0.8	0.6	–	0.1	0.1
6.5–6.9	3.1	2.5	3.0	2.0	0.4	0.3	–
7.0–7.4	31.6	20.5	20.1	9.8	5.0	3.6	2.8
7.5–7.9	36.7	37.3	32.3	30.2	24.8	18.3	11.5
8.0–8.4	15.0	23.3	19.9	26.1	36.7	32.4	28.7
8.5–8.9	6.8	8.9	11.5	15.6	22.4	21.7	24.3
9.0–9.4	4.1	4.3	7.3	8.3	8.4	13.0	17.0
9.5–9.9	1.6	1.6	3.4	3.8	2.0	6.1	10.2
10.0–10.4	0.5	0.3	1.1	1.9	0.3	3.3	3.7
10.5–10.9	T	0.1	0.2	0.4	–	1.0	1.3
11.0–11.4	–	T	0.1	0.1	–	0.1	0.2
11.5–11.9	–	–	–	–	–	0.1	0.2
Avg length:	7.74	7.86	7.98	8.14	8.25	8.49	8.68
No. of fish:	3,570	4,228	16,454	2,077	1,039	1,226	1,635

27% from that of the comparable period in 1962. The increase between 1964 and 1965 probably reflects recovery of the market after the botulism scare and the sharp increase in availability of large bloaters (Tables IV and V).

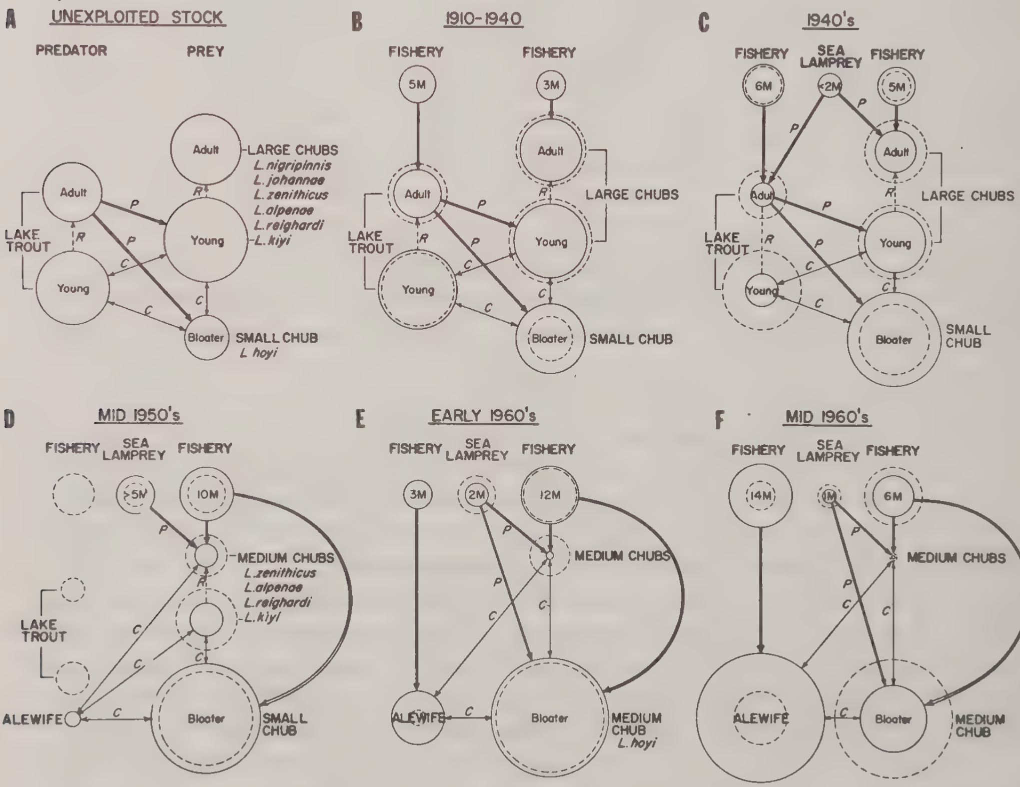
INTERACTION AMONG DEEPWATER SPECIES

There is little question that the selective fishery in the Great Lakes has had a substantial influence on the interaction among various species (Hile, 1954). When ecological relationships are disturbed by selective fishing so that the reduction of some species gives a competitive advantage to others, a population imbalance is created and a rapid succession of species can follow. It is difficult to separate successions induced by environmental changes from those caused by exploitation because both factors are usually involved. The deepwater area of Lake Michigan has had no conspicuous environmental changes except in fish populations, however, and provides a good illustration of the interaction and succession of species influenced primarily by exploitation.

Unexploited stocks.— The Great Lakes are young; during less than 10,000 years in their present form they have developed a very simple deepwater fish fauna. The lake trout was the principal climax predator and it fed mostly on the young of six species of large chubs and a small slow-growing chub bloater (Fig. 5A). Adults of the larger chubs were mostly too large for prey of lake trout and provided a breeding stock that added stability to the predator–prey balance.

The burbot was the only other predator in the deepwater region but it was less abundant than the lake trout. The lake trout and burbot also preyed heavily on the deepwater sculpin (*Myoxocephalus thompsonii*) and to a lesser extent on the ninespine stickleback (*Pungitius pungitius*) in the northern end of the lake (Van Oosten and Deason, 1938). Measures of abundance are not available for the burbot, sculpin, and stickleback and they cannot be included in this discussion, but it can be assumed that the burbot underwent changes similar to the lake trout. There has been no evidence of major change in the abundance of the deepwater sculpin (which occupies a very limited niche close to the bottom in the deeper areas thoughout the lake) or of the stickleback (largely restricted to the northern section of the lake).

Stable fishery, 1910–40.— The introduction of a lake trout fishery which underwent an initial increase and several subsequent levels of stability (Hile et al., 1951a) undoubtedly had the usual effect on a newly exploited stock



A
UNEXPLOITED STOCK
PREDATOR
PREY
Adult
LARGE CHUBS
L. nigripinnis
L. johannae
L. zenithicus
L. alpenae
L. reighardi
L. kiyi
Adult
LAKE TROUT
Young
Young
Bloater
SMALL CHUB
L. hoyi
P
R
C
B
1910-1940
FISHERY
FISHERY
5M
3M
Adult
LARGE CHUBS
Adult
LAKE TROUT
Young
Young
Bloater
SMALL CHUB
C
1940's
FISHERY
SEA LAMPREY
FISHERY
6M
2M
5M
Adult
LARGE CHUBS
Adult
LAKE TROUT
Young
Young
Bloater
SMALL CHUB
D
MID 1950's
FISHERY
SEA LAMPREY
FISHERY
>5M
10M
MEDIUM CHUBS
L. zenithicus
L. alpenae
L. reighardi
L. kiyi
LAKE TROUT
ALEWIFE
Bloater
SMALL CHUB
E
EARLY 1960's
FISHERY
SEA LAMPREY
FISHERY
3M
2M
12M
MEDIUM CHUBS
ALEWIFE
Bloater
MEDIUM CHUB
L. hoyi
F
MID 1960's
FISHERY
SEA LAMPREY
FISHERY
14M
1M
6M
MEDIUM CHUBS
ALEWIFE
Bloater
MEDIUM CHUB

FIG. 5. Interrelations of major deepwater species of Lake Michigan before exploitation (A) and during the following periods: stable exploitation, 1910–40 (B); early influence of the sea lamprey, 1940's (C); maximum abundance of the sea lamprey, mid-1950's (D); maximum abundance of bloaters, early 1960's (E); maximum abundance of the alewife, mid-1960's (F). P = predation; C = food competition; and R = recruitment.

composed of many age-groups, and reduced the number of older and larger fish (Ricker, 1963). Data are lacking but scattered accounts indicate clearly that the largest lake trout were reduced and became legends by 1927–39 when the catch stabilized at about 5 million lb (Hile et al., 1951a). Since the lake trout experienced no major fluctuations it can be safely assumed that the stocks were not overexploited and that the population underwent the typical adjustment to lower average age, increased growth rate, and more rapid recruitment of young to adults which compensated for the exploitation of the fishery (Fig. 5B).

A modest fishery for chubs that fluctuated about a usual catch of some 3 million lb had a similar influence on the chub stocks. Two of the largest species of chubs, however, were selected strongly by the fishery and were reduced greatly by the early 1900's (Hile and Buettner, 1955). This reduction was apparently compensated by an increase in the representation of bloaters in the chub stocks as measured during a fishery survey in 1930–32 (Moffett, 1957). The increase in abundance of bloaters would have offset any reduction of young of the larger chubs that served as prey for lake trout, and thus contributed to the stability of the lake trout stock and the lake trout fishery.

Establishment of the sea lamprey, 1940's.— The sea lamprey became established in the deepwater population in small but significant numbers during the 1940's. Although the sea lamprey undoubtedly preyed on all large fish in the deepwater area (lake trout, burbot, and adults of large chub species), their effect on the lake trout population was swift and drastic. The estimated pounds of fish killed by the sea lamprey annually in the 1940's was small in comparison with later years and may not have exceeded 2 million lb at the end of the decade (Table III). Sea lamprey predation certainly must have been comparatively small when the lake trout catch started to decline about 1945 (Fig. 3). The increased exploitation by the fishery during the period immediately preceding the decline of lake trout, however, could have made the lake trout stock of Lake Michigan particularly sensitive to the predation by the sea lamprey.

As the lake trout declined, its predation on small chubs decreased and the sea lamprey predation turned from lake trout to the adults of large chubs. The fishery also transferred to large chubs as lake trout declined (Fig. 4). Thus the deepwater stocks of Lake Michigan, after supporting a stable fishery since its beginning, entered a period of instability favoring bloaters (Fig. 5C) which according to complaints of commercial fishermen had started to become a nuisance in their nets by 1950.

Sea lamprey maximum, mid-1950's.— Fishery surveys of Lake Michigan during 1950–55 showed that the two largest chubs had become nearly extinct; that the four remaining species of larger chubs were greatly reduced; that bloaters constituted over 75% of the chub population (Moffett, 1957); and that lake trout were near extinction (Eschmeyer, 1957). By the mid-1950's the sea lamprey population had reached maximum abundance; the estimated destruction exceeded 5 million lb of fish per year (Table III), primarily large chubs. In this period of peak abundance, the sea lamprey was also observed more frequently in shallower areas of the lake where it preyed heavily on whitefish, suckers, and walleyes (*Stizostedion vitreum*), all of which suffered sharp reduction in stocks. The deepwater fishery which had only chubs to catch increased to over 10 million lb during 1951–57, the period of the sea lamprey maximum. The large chubs were preferred by the fishery but were insufficient to fill the demand so the larger bloaters started to enter the catch for the first time and were marketed as a "No. 2 chub" at a lower price.

The events of the mid-1950's produced great instability in the balance of deepwater species, created a strong pressure against the large chubs, and favored bloaters despite the first substantial exploitation of larger bloaters by the fishery (Fig. 5D). An almost unnoticed but significant event in the early 1950's was the establishment of the alewife which was first reported in 1949. No alewives were taken in extensive experimental trawling in southern Lake Michigan in 1954, but eight alewives were taken during a survey throughout the northern part of the lake in 1955. Over 45,000 and 38,000 alewives were taken in experimental trawls during similar surveys of southern and northern Lake Michigan in 1960 and 1961, respectively.

Bloater maximum, early 1960's.— Bloaters dominated the chub population even more strongly according to surveys in 1960–61, when they constituted 93–95% of the chubs taken in experimental gillnets (Smith, 1964). The abundance of bloaters had increased in the latter period at four of the seven locations used for 1954–55 and 1960–61 comparisons. The size of bloaters had increased during this period (Tables IV and V) and, since the largest individuals of the other species of chubs were gone, much of the ecological and fishery significance of size differences among species of chubs had been lost. Also exploitation of all sizes of chubs started with the initiation of trawling, as chubs constituted well over half of the catch taken by trawls in 1960–61 when the total chub catch had reached record highs above 12 million lb (Table III). The larger chubs of all species were still preferred, however, and were exploited heavily by the gillnet fishery. The sea lamprey, which had suffered a population decline as its prey declined, still destroyed more than 2 million lb of fish annually in the early 1960's.

Thus, the pressures had shifted to bloaters but continued heavy on the small populations of the four larger chub species that remained in the lake (Fig. 5E). The alewife was the only species present in deeper areas of the lake that could be favored by the selection against chubs. It had become well established throughout the lake by the early 1960's and supported an expanding fishery of about 3 million lb.

Alewife maximum, mid-1960's.— The competitive advantage of the alewife which resulted from heavy exploitation of chubs of all sizes undoubtedly speeded a population explosion of alewives that gained its greatest impetus in the early 1960's. The number of young-of-the-year alewives taken in comparable trawling during early November in southern Lake Michigan increased 56 times between 1962 and 1964, and the number of adults increased 5 times between 1962 and 1966 (Table VII). The small change in abundance of adults, the increase in average age of the adult stock between 1965 and 1966, and the failure of the extremely large 1964 year-class to increase the adult stocks in 1966 indicate clearly that the alewife population was approaching saturation.

The great abundance of alewives and a continuing heavy exploitation of chubs had placed the chubs at a strong disadvantage by the mid-1960's (Fig. 5F). It is not certain if the fishery for alewives that reached 29 million lb in 1966 was large enough to influence the alewife stocks sufficiently to affect their competitive advantage.

Measures of the abundance of chubs have not been available since 1960–61 but the dominance of bloaters continued to increase, and they constituted 99.2% of all chubs taken in experimental trawls during 1964 (Wells, 1966). Evidence also exists of a biological change of uncertain causes that may reflect an ecological stress for bloaters. In addition to the marked increase in size of bloaters which reflects the combined effect of faster growth and an increase in average age in recent years, there has also been a continued increase in percentage of females in the population. The proportion of females in the population reached 97–99% during various months in 1966.

An increase in size has accompanied declines in populations of the lake herring, a close relative of the bloater. The size and growth rate of the lake herring of Lake Superior increased during early stages of a recent decline in numbers of fish in the stock in 1950–62 (Dryer and Beil, 1964), and the size has continued to increase as the abundance declined sharply after 1962. A well-documented study of the collapse of a lake herring population in Birch Lake, Michigan, showed that an increase in growth and size of fish in the population, and a strong dominance of females (84–93%) preceded a sharp decline in 1945–46 (Clady, 1967). Although data are lacking, the collapse of lake herring stocks of Lake Michigan in the late 1950's also was accompanied by observations of fishermen and biologists of a progressive increase in the size of fish taken in the fishery. The lake herring of Lake Michigan were presumed to have declined as a result of early establishment of alewives in shallow water (Miller, 1957). Such evidence implies that the recent biological changes of the bloater stocks of Lake Michigan may be indicators of a pending collapse of the population. There is no indication among coregonids that these changes have stopped or reversed until after the population has declined.

Establishment and Dominance of the Alewife

The alewife has been the only fish in the Great Lakes that has occupied all sections of a lake and its bays, estuaries, and tributaries in great numbers. It has become the most abundant and widely distributed species in Lake Michigan where it has displaced all major planktivorous species. Although studies are lacking, similar dominance of the lake and other species appears to have occurred in Lakes Ontario and Huron.

The alewife was first recorded in the Great Lakes in Lake Ontario in 1873 and has been abundant there since the late 1800's. Just how the alewife

TABLE VII. Abundance of adult and young-of-the-year alewives in Lake Michigan at Saugatuck, expressed as catch per 10-min trawl tow and as effective catch per unit of effort (CPE) for depths of 3–40 fath during early November in 1962–66.

	Young-of-the-year					Adult				
Depth	Nov. 8, 9, 1962	Nov. 7, 9, 1963	Nov. 4, 1964	Nov. 10, 1965	Nov. 15, 1966	Nov. 8, 9, 1962	Nov. 7, 9, 1963	Nov. 4, 1964	Nov. 10,[a] 1965	Nov. 15,[b] 1966
3	–	12	1714	2340	0	–	64	18	406	80
5	7	254	1478	2638	4	294	182	176	260	514
7	27	357	2599	2500	42	18	111	28	657	911
10	48	25	107	946	587	80	52	198	803	752
12	–	78	319	925	518	–	62	238	497	429
15	74	299	1591	22	320	12	107	308	507	534
17	30	204	1989	0	462	110	42	204	798	805
20	28	5	5863	0	2	26	74	396	507	529
25	4	3	0	0	2	57	206	106	227	400
30	0	0	0	0	1	76	60	34	232	219
35	0	0	1	0	0	182	14	52	156	84
40	0	0	0	0	0	1	12	56	143	141
Effective CPE[c]	31	137	1740	1562	215	86	82	151	432	450

[a] Percentage age composition: I, 2%; II, 73%; III, 25%.
[b] Percentage age composition: I, 1%; II, 59%; III, 38%; IV, 2%.
[c] Average catch for depths at which fish were taken.

got into Lake Ontario is uncertain. It long had free access to the lake via the St. Lawrence River from its native habitat along the Atlantic Coast. It seems that the alewife would have appeared in Lake Ontario much earlier if it had followed this route. It is more likely that alewives that became established in Lake Ontario were included in shipments of young American shad (*Alosa sapidissima*) that were planted in Lake Ontario in the early 1870's (Woods, 1960).

After its establishment in Lake Ontario, the movement of the alewife to the other Great Lakes was slow. Niagara Falls was a natural barrier to fish migration between Lakes Ontario and Erie before the completion of the Welland Canal in 1829. Contrary to common belief, this canal did not provide an easy route for fish to bypass Niagara Falls. Its many locks, which raise ships 327 ft between Lakes Ontario and Erie, impose partial barriers and the strong downstream currents created as the huge locks are emptied repeatedly, are major deterrents to upstream migration. The sea lamprey, a native of Lake Ontario, took nearly 100 years after the canal was opened to appear in Lake Erie in 1921 (Applegate, 1950), and the alewife did not appear in Lake Erie until 1931 — 58 years after it was first found in Lake Ontario. When the alewife reached Lake Erie it had free access to all of the other Great Lakes. It was first found in Lake Huron in 1933, in Lake Michigan in 1949, and in Lake Superior in 1954.

The alewife was common in Lake Erie by 1942, but it probably did not become extremely abundant there. The deep water where the alewives concentrate in winter to avoid unfavorably cold water is limited in Lake Erie and the lake has always had a large population of predators. Lake Huron also had a large population of lake trout and burbot that would have preyed on the alewife when it entered the lake in the 1930's, but these were virtually eliminated from the lake during the mid-1940's by sea lamprey predation. Subsequently the alewife became very abundant by the mid-1950's and increased irregularly until 1964 (Coble, 1967).

The alewife has spread throughout Lake Superior but has not yet become abundant and its future there is uncertain. The lake not only has a large population of predators, but is the coldest of the Great Lakes — and cold does not favor the alewife.

The sea lamprey had almost eliminated the large predators in Lake Michigan when the alewife was first recorded there in 1949. The alewife had strong competitive advantage over other planktivorous species because of its efficient filter-feeding behavior and its characteristic of forming dense schools that occur in all areas of the lake during different seasons.

The alewife increased rapidly in Lake Michigan during the 1950's; it was first noted in abundance in Green Bay in 1953, and was abundant throughout the lake in 1956. During recent years the adult population has more than doubled each year. Obviously this rate of increase could not continue as each new hatch of young encounters an increasingly greater population density and more competition for food and space. Scattered data on age composition indicates that a decreasing percentage of young survived to become adults as the population increased. As this trend continues to a point where the number of adults is so great that it becomes very difficult for young to survive, the number of young reaching adulthood starts to decrease and the population reaches a peak. Evidence indicates that the population had reached this point during 1966–67.

Because the alewife occupies various sections of the lake in dense schools during different seasons, it can influence all other species of the lake. In mid-winter the adult alewives are densely concentrated on the bottom in the deepest areas (Wells, 1968), where they seek the warmest waters. This area was occupied by the kiyi (*L. kiyi*), which was abundant as recently as 1954–55 (Moffett, 1957), but had become greatly reduced by 1960–61 (Smith, 1964), and was nearly extinct by 1964 (Wells, 1966).

In late winter and early spring the alewives move toward shore in dense schools that pass through the region occupied by the bloater (Wells, 1968). This region is also occupied by the alewife in the fall as it returns to deep water. Although the bloaters increased greatly during the 1950's (Moffett, 1957; Smith, 1964), their abundance has been decreasing sharply in the 1960's as alewives increased.

During the late spring and summer the adult alewives are concentrated in the shallower areas (Wells, 1968), where they spawn near shore and in rivers and bays during June and July. The lake herring and the emerald shiner (*Notropis atherinoides*), which previously were extremely abundant in the shallow areas and bays of the Great Lakes, decreased sharply in various areas as alewives became established (Miller, 1957) and were very scarce or absent after the alewife reached extreme abundance in Lake Michigan (Wells, 1968).

The yellow perch (*Perca flavescens*) which occupies the inshore area became more abundant as the alewives increased in Lake Michigan. The increase in abundance and resultant stimulation of effort were reflected by an increasing catch of perch during the early 1960's that reached 5.8 million lb in 1964. The increase in yellow perch may have resulted from the greater supply of food that the alewives provided for larger perch. As alewives became very abundant they crowded the shore in dense schools during spring and summer and the yellow perch moved further from shore. The concentration of alewives near shore, and the displacement of yellow perch occurred during the spawning and hatching period of the yellow perch, and as the alewives became very abundant during the early 1960's recruitment of perch must have been affected as the abundance of adult perch dropped sharply. This was reflected by the sharp decline of the catch of yellow perch to 1.3 and 0.7 million lb in 1965 and 1966, respectively.

The American smelt which also occupied the inshore areas of the lakes declined sharply when alewife abundance increased. The smelt production in Lake Michigan declined from a peak of about 9.1 million lb in 1958 to 0.9–1.2 million lb since 1963. Because the American smelt is still abundant in Lake Ontario where the alewife has long been the dominant fish, it seems unlikely that smelt will be influenced as strongly by the alewife as were the chubs, lake herring, and emerald shiners, all of which are very scarce in Lake Ontario.

During the fall and winter after hatching, the young alewives occupy the mid-depths of the lake where they remain until their third summer (age II) before moving to the bottom. The midwater area has also been the zone occupied by the young lake herring, chubs, and American smelt during their first 2 years. Undoubtedly the competition between the young of the alewives and the young of other species was severe as the alewives reached great abundance.

The occupation of various zones of the lake in different periods by dense congregations of alewives has changed greatly the utilization of the invertebrate productivity by fish. The chubs, lake herring, emerald shiners, yellow perch, and American smelt were abundant species that occupied various sections of the lake and were major consumers of invertebrates throughout the year. Under present conditions when the alewife is concentrated inshore in the summer, the deepest zone previously inhabited by the kiyi in great abundance (Hile and Deason, 1947) is essentially unoccupied by an abundant species and the invertebrate food is incompletely used. Similar situations occur during other seasons when sections of the lake vacated by the alewives as they move from zone to zone are left with greatly reduced populations of the species that once occupied each section in great abundance throughout the year. As abundant as the alewife is, and despite its apparent intensive use of the invertebrate food of each zone of the lake during different seasons, I believe it unlikely that the biomass represented by the alewife is equal to the total of all of the previously abundant species that it has displaced.

Reestablishment of Climax Predators

The unprecedented instability of fish stocks in Lake Michigan in the mid-1960's at a time when the alewife fishery is continuing to expand and climax predators are being reestablished certainly will result in continued rapid change. Although the alewife catch reached 29 million lb in 1966 and may reach 50 million lb in 1967, processing facilities that exist can handle approximately 100 million lb. Despite the heavy annual die-off of alewives each spring that was the greatest on record in 1967, alewives continued to be plentiful during the summer of 1967. It is uncertain if the fishery approached full exploitation of the alewife stocks at their peak. Early decrease in alewife stocks seems likely, however, due to over-population and a sharp increase in mortality between the end of the 1st year and entry into the adult stocks, as illustrated by the fewer adults that entered the stocks at age II from the very large 1964 year-class (266 in 1966) than from the much smaller 1963 year-class (315 in 1965; Table VII).

A vigorous program is underway to reestablish climax predators in Lake Michigan to create a predator–prey balance with the alewife. Sea lamprey control in Lake Michigan was initiated in 1960 and was effective in 1967.

Lake trout stocking by the states and federal government started in 1965, has reached nearly 2 million fingerlings annually, and will be continued until natural reproduction is well etablished. Michigan stocked 660,000 fingerling coho salmon (*Oncorhynchus kisutch*) in Lake Michigan in 1966, and 1,700,000 coho and 800,000 chinook salmon (*O. tshawytscha*) in 1967. The survival of coho salmon as indicated by spawning runs of adults from the 1966 plant and precocious males of the 1967 plant indicate unusual success. Michigan and Wisconsin are increasing their plants of steelhead trout (*Salmo gairdneri*) in Lake Michigan tributaries. The coho salmon are occupying the upper strata of the lake and are feeding heavily on the young alewives that live at middepths. This region is apparently where the steelhead trout and chinook salmon will feed most heavily as neither are taken on the bottom in deeper water.

The Province of Ontario has started to make large introductions of splake in Lake Huron and these fish will have free access to Lake Michigan if successful. The splake is a hybrid of lake trout and brook trout (*Salvelinus fontinalis*) that has been selected for several generations to develop a strain that will occupy deep water, grow fast, and mature early. Michigan and Ontario have also initiated experimental introductions of kokanee (*Oncorhynchus nerka*) in the Lake Michigan watershed and in Georgian Bay of Lake Huron. Although it is uncertain where the kokanee will live in the Great Lakes, they will probably compete with the alewife for food.

It seems unlikely that all of these species can be established with equal success as the productivity of Lake Michigan has not changed greatly over the pre-sea lamprey period. The closed ecosystem of a lake differs greatly from the native ocean habitat of the salmon, and competition among the various species of salmon and trout for the available food will undoubtedly become intense as their numbers increase. It is uncertain yet which predators will have a biological or competitive advantage over others, but it does appear that the predator–prey relation will be unstable as long as the alewife remains the single dominant prey species. In fact, it seems likely that the fishery productivity may be lowered from the pre-sea lamprey period because of the instability of the predator–prey balance, and apparent less-efficient use of the invertebrate food of the entire lake by the alewife than by the previous multiple-species complex.

Greater stability and full productivity of Lake Michigan, and other Great Lakes that have been similarly affected by recent events, can only be achieved by careful regulation of the kinds and numbers of predators, and the reestablishment of a multiple-species complex of prey species. Since the greatest stability occurs at low population density, management of the lakes to obtain the highest yield will require continuous surveillance and manipulation of all species to prevent onset of uncontrolled instability and recurrence of extreme imbalances in the future.

To manage the fishery resource for high yield, both recreational and commercial fisheries must be closely regulated and the amounts of various species taken by each must be closely controlled with respect to the potential yield of each species and the expected interactions among competing predator or prey species that are not fished heavily or selectively. It may also be necessary to create or induce fisheries for species not involved directly in the predator–prey balance of the lakes, but which could be favored by short- or long-term changes of the environment.

An essential requirement for successful and continued restoration of a useful fishery balance is uniformity in management approach among the states and Canada which own and manage the fisheries in their respective sections of the various lakes. Management objectives for individual lakes or adjoining lakes must be compatible and regulations and management procedures closely integrated.

The potential of common attack on problems of the Great Lakes is illustrated by the highly successful interstate and international program to control the sea lamprey and rehabilitate the lake trout that has been, in fact, the first step toward the achievement of a new and more favorable ecological balance among fish stocks.

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the ALEWIFE

by Stanford H. Smith

Biological Laboratory
U.S. Bureau of Commercial Fisheries
Ann Arbor, Michigan

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That Little Pest

the ALEWIFE

by Stanford H. Smith

When the first alewife, *Alosa pseudoharengus*, was discovered in Lake Michigan near South Manitou Island on May 5, 1949, few people would have guessed that it would become the best known fish of the lake in less than two decades. Now it competes only with the coho salmon in its claim to such fame. When the third specimen was officially recorded from Milwaukee, Wisconsin, in March 1952, however, a newspaper story carried a somber warning from a knowledgable yet anonymous official of the Michigan Department of Conservation that the alewife might raise havoc with the native species. This warning was fully justified by fact in the years to follow. An upset of the entire fishery ecology of Lake Michigan was already well under way in 1949 when the sea lamprey was consuming the last vestiges of the lake trout *(Salvelinus namaycush)* and burbot *(Lota lota)*—the only abundant and widely distributed predators of the lake. Absence of large predators left the way wide open for a small and prolific species such as the alewife. Under this condition the alewife increased with almost unbelievable swiftness. In 1960 alewives represented about 8 per cent of the poundage of fish taken in experimental trawls in Lake Michigan; by 1966 they represented over 80 per cent. When undergoing its increase the alewives have reduced or replaced all of the previously very abundant species of the lake, and upset completely a very productive and stable multiple-species balance that had existed since the glaciers retreated from the Great Lakes thousands of years ago.

Alewives are more widely known for their obnoxious habit of dying off and littering the beaches than for the extensive biological changes that they have brought about. They make a massive movement toward shore in early spring after spending the winter in the deepest areas of the lake. Shortly after reaching shallow water they start dying off in large numbers. Their dead carcasses wash up on the beaches to rot much to the distress of bathers, lakeshore residents, and resort owners. Even live alewives that crowd the shore in the early spring cause great distress by clogging intakes of municipal water plants, power plants, and industries that draw vast quantities of water from the lakes.

Why alewives die is still not understood and the number of theories almost equals the number of people who express them. Before we evaluate the theories about why alewives die it is necessary to point out that the alewife is not naturally a freshwater fish. It is a marine fish that is anadromous, which means it normally grows up and spends its adult life in the ocean and enters freshwater only to spawn. Soon after hatching the young move back out to the ocean where they grow up and mature. Some alewives in their native ocean environment die after going through the rigors of spawning, but they do not all die as do the Pacific salmon, and a great many return to spawn in the ensuing years. In fresh water most mature alewives die before they spawn even once.

Although alewives have been able to complete this entire cycle in fresh water, they seem to do it with difficulty. The only normal part of the cycle completed in lakes is the spawning, hatching, and early life which is, in fact, in fresh water exactly as it is in their native environment. It is significant that this "natural" part of the cycle in fresh water is highly successful; the adults encounter little difficulty or mortality in spawning and the young hatch and thrive with great success. Thus, it is in the "unnatural" part of their existence in the Great Lakes when they encounter difficulties—growing up in fresh water rather than the salty ocean.

Clues to Death

The differences between their ocean and freshwater environments might give some clues about why alewives experience their regular and massive mortalities during the unnatural segment of their life in fresh water. An analysis of the native range and habits of alewives reveals that they avoid cold water. They are most abundant in the middle Atlantic region of the east coast of North America, and uncommon in the colder waters of the Gulf of the St. Lawrence and the more northerly extremities of their range off Labrador. Thus, in their native environment alewives apparently shun the low temperatures that they cannot escape in midwinter when confined to freshwater life in the Great Lakes. Some alewives have been observed to die when subjected to temperatures below 38° F and this is undoubtedly why they must seek the deepest areas of lakes in midwinter where the water is warmest—usually 39° F. The fact that deep water in the Great Lakes can become colder than this during severe winters may explain why alewives sometimes start to die in the deepest waters in midwinter. Such dieoffs have been observed in Lakes Ontario, Erie, and Michigan, and were particularly severe in Lake Michigan in the winter of 1966–67 where measurements in early spring indicated that deepwater temperatures may have been lower than usual. Midwinter dieoffs go unnoticed because most fish remain on the bottom and do not wash ashore. These dieoffs are almost unknown except to biologists who study the lakes, and to commercial fishermen who are bothered by the dead fish in their nets. The influence of occasional winter dieoffs on the alewife population is unknown but the more regular spring dieoffs have the greatest impact on the general public and always cause major changes in the population when they occur.

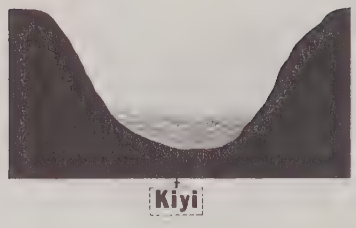
Too Many

Why do alewives die in such great numbers in the spring? The number of alewives must be a factor as there is no conspicuous dieoff when alewives are not extremely abundant. Dieoffs were not a problem in Lake Michigan until the late 1950's although alewives were abundant enough in 1956 to start a commercial fishery. There have been large schools of alewives scattered throughout Lake Superior for the past five or six years but no conspicuous dieoffs have occurred. Even in Lake Ontario where troublesome dieoffs have been experienced since about 1875 there have been years when dieoffs have not been a problem. It appears then that a great number of alewives may be necessary before conspicuous and troublesome dieoffs occur. At low densities some dead alewives are seen in the spring, but there may be so few that they are cleaned up by seagulls before they reach the shore.

Temperature Adjustment

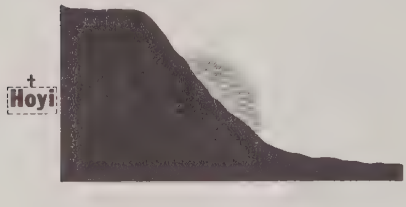
The difficulty that alewives have in adjusting to temperature change seems to be a more important factor related to the spring dieoff. This relation has been noticed by the many investigators who have made extensive studies of alewife dieoffs over past decades. To reach the shallow inshore areas and rivers where alewives spawn in late spring and early summer they must move from the cool water of the open lake to the warmer shore and river water. The most conspicuous example of the difficulty that alewives experience when encountered with a sharp temperature change occurs on calm days when warmer river water mushrooms out into the lake and forms a sharp interface with the cooler lake water. Wherever this happens when alewives are concentrated near shore, a "fairy ring" of dead and dying alewives appears along the line where river and lake water meet. At the same time, however, the alewives in both the cooler lake water and warmer river water are active and seem to be experiencing no difficulties. Such neat examples are rare, for the interface between warmer inshore or river water and cooler offshore water is irregular and often extends far out into the lake. During these periods alewives appear to be dying everywhere. Alewives may experience trouble with another kind of temperature change in areas of intensive local dieoffs during the summer. Up-

Winter



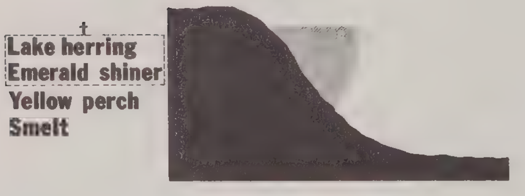
In the Winter *adult alewives live in the deepest water where they have nearly replaced one chub known as the kiyi.*

Spring & fall



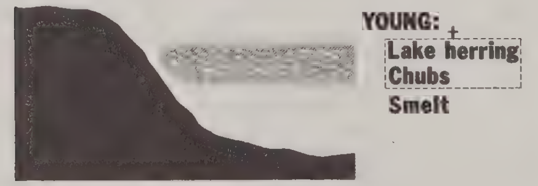
In the Spring and Fall *the alewives pass through the nearshore mid-depths, where they are eliminating another chub, the hoyi.*

Summer


†
Lake herring
Emerald shiner
Yellow perch
Smelt

In the Summer, *when alewives crowd the shore, the lake herring and emerald shiner have become very scarce and the yellow perch and smelt are reduced.*

All year (young)


YOUNG:
†
Lake herring
Chubs
Smelt

All Year *the young alewives can be found in the central middepths of the lake, where they spend their first two years. They have competed severely with lake herring, the two species of chubs, and smelt.*

Illustrations by Paul M. Earl

wellings of deep cold water are common near the shore of Lake Michigan during the summer when wind conditions are just right. These upwellings can trap the alewives in the warm water near shore. The longer the upwelling lasts, the closer the cold water moves to shore, until the shore water itself is cold and the alewives have no escape.

Thyroid Deficiency

The question of why alewives that live their entire lives in fresh water cannot adjust to temperature change must be determined by laboratory research, but a clue has already been discovered. Although alewives in their natural life cycle often suffer mortalities, these dieoffs occur irregularly and are not clearly associated with accommodation to temperature change. A very conspicuous difference has been discovered between the condition of the thyroid gland in ocean alewives and that in freshwater alewives which may affect temperature accommodation. The thyroid gland of alewives in the ocean is healthy and normal, but the thyroid of the adult freshwater alewife appears exhausted. The thyroid exhaustion of freshwater alewives may be caused by the difference in the amount of iodine present in the water. Iodine is an important constituent in the salt water of the ocean, but present in only very minute quantities in fresh water. Iodine is essential for the normal function of the thyroid of all animals and its lack may be responsible for the poor condition of the thyroid of the alewife in fresh water. Little is known about the purpose that the thyroid serves in fish, but in other animals it is known to be very important in regulating metabolism—adjustment to heat and cold, regulation of body fluids and chemistry, and the complex processes of growth and sexual development. Thus, the thyroid deficiency of the freshwater alewife may prove to be one of the important factors in the difficulties that confront the alewife in its unnatural years of growth and maturity in fresh water which, in the end, leads to extreme stresses that contribute to the massive dieoffs.

There are suggestions of other factors that may cause dieoffs, however. Oxygen depletion has been suspected where alewives are extremely dense and dying off in great numbers in inshore waters. The amount of oxygen that is dissolved in water may be lowered but no critically low levels have been measured. That oxygen depletion caused by an extreme abundance of alewives may not be a serious problem is illustrated by the dense concentrations of alewives in confined areas of warm and rich water at times when alewives are not dying. A striking example occurs each spring between the breakwaters of the Kalamazoo River where it enters Lake Michigan. Alewives become so concentrated in this narrow stretch that it almost seems that you can walk on them. Trawlers that fish the area dare not tow their nets more than a few minutes or the catch will be so great that it cannot be landed without swamping their vessels. Certainly the alewives must reduce the oxygen concentration when they are so dense, but not sufficiently to cause them to die.

Another Theory

Another theory that has been proposed is that alewives are killed by the poisonous properties of blue-green algae which has become more prevalent during recent years in the richer inshore water where dead alewives are observed. Although the poisons of blue-green algae may contribute to the difficulties that cause alewives to die in richer areas during recent years, it is unlikely that blue-green algae was a factor in dieoffs in the still clean, clear waters of Lake Ontario in the late 1800's. The probable significance of the contribution of blue-green algae to the dieoff is also lessened because alewives continue to be very abundant in the inshore waters after the dieoff, when these waters have been made even more favorable for blue-green algae by the enrichment resulting from the dead fish.

Starvation a Cause?

Food shortage and starvation have also been suggested as contributors to the dieoff. This theory is prompted by the thin appearance of the alewives which gives the impression that they are emaciated. Very thin bodies are characteristic of alewives during all seasons. Cursory examinations have shown that the percentage of alewives with food in their stomachs is about the same among dead and dying alewives as among healthy ones. Alewives have been known to reduce the food supply, however, and reduced food intake or nutritional deficiency may add to other factors of dieoff.

A fungus is often found on dead and dying alewives but this fungus is common on many species of fish when they are sick, weak, or stressed. Since many dead and dying alewives lack fungus, it is not the sole cause of the dieoff, but undoubtedly it is an infestation related to the dieoff. Pollution and warm water also have been suggested as factors contributing to dieoff, but adults live and spawn without dying in the warmest bays and rivers that are heavily contaminated with wastes. The eggs hatch and young thrive in these areas. Spawning itself has been thought to be a factor but dead or dying alewives are seldom seen in areas where spawning is taking place, and—as pointed out in a study of the alewife dieoffs in Lake Ontario in the 1880's—a dead alewife that has spawned is rarely seen.

Ominous Implications

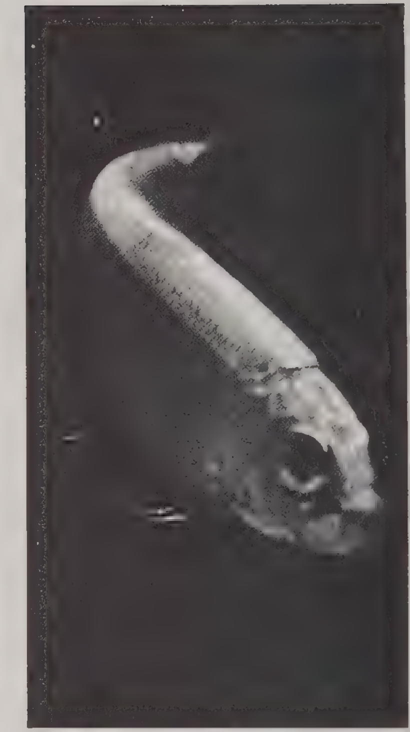
As troublesome as the dieoffs have been the alewife has caused even greater and more serious problems in the fishery ecology of our lakes, and has seriously reduced the value of the lakes as a stable and productive fishery resource. The history of the alewife in the Great Lakes is a story in itself and one with more far-reaching and ominous long-range implications than the short-term distress caused by dieoffs.

The alewife was first recorded in the Great Lakes in Lake Ontario in 1873 and has been very abundant there since the late 1800's. Just how the alewife got into Lake Ontario is uncertain. It long had free access to the lake via the St. Lawrence River from its native habitat along the Atlantic Coast. It has never been abundant in the lower St. Lawrence River, however, and it seems that it would have appeared in Lake Ontario much earlier if it had followed this route. It is more likely that the alewives which became established in Lake Ontario were accidently included in shipments of young Atlantic shad that were planted in Lake Ontario about 1870.

After its establishment in Lake Ontario, the movement of the alewife to the upper Great Lakes was slow. Niagara Falls was a natural barrier to fish migration between Lakes Ontario and Erie before the completion of the Welland Canal in 1829. Contrary to common belief, this canal has not provided an easy route for fish to bypass Niagara Falls. Its many locks, which raise ships 327 feet from Lake Ontario to Lake Erie, impose partial barriers, and the strong downstream currents created as the huge locks are repeatedly emptied are major deterrents to upstream migration. The sea lamprey *(Petromyzon marinus)*, a resident of Lake Ontario since postglacial time, also had difficulty making its way through the Welland Canal. It was nearly a century after the canal was opened before the sea lamprey first appeared in Lake Erie in 1921. The alewife did not appear in Lake Erie until 1931—58 years after it was first found in Lake Ontario. When the alewife reached Lake Erie it had easy access to all of the other Great Lakes. It was first found in Lake Huron in 1933, in Lake Michigan in 1949, and in Lake Superior in 1954.

Avoids Cold Water

The alewife was common in Lake Erie by 1942, but it did not become extremely abundant there. The deep water where the alewives concentrate in winter to avoid unfavorably cold water is limited in Lake Erie and the lake has always had a large population of predators. Lake Huron also had large population of lake trout and burbot that would have preyed on the alewife when it entered the lake in the 1930's, but these were virtually eliminated from the lake during the mid-1940's by sea lamprey predation. Subsequently the alewife became very abundant by the mid-1950's. Records of experimental fishing by the Ontario Department of Lands and Forests show that the alewife increased irregularly in South Bay, Lake Huron, until 1964.



Bureau of Commercial Fisheries

A Young Alewife *poses cautiously at the Bureau of Commercial Fisheries research laboratory in Ann Arbor.*

The alewife has spread throughout Lake Superior but has not yet become abundant, and its future there is uncertain. The lake has a large population of predators because the sea lamprey has been controlled since 1961, and lake trout have returned to near pre-lamprey abundance. Lake Superior is also the coldest of the Great Lakes—and cold does not favor the alewife.

The sea lamprey had almost eliminated the large predators in Lake Michigan when the alewife was first found there in 1949. The alewife had strong competitive advantage over other planktivorous species because of its efficient filter feeding and characteristic of forming dense schools that occur in all areas of the lake during different seasons.

The alewife increased rapidly in Lake Michigan during the 1950's; it was first noted in abundance in Green Bay in 1953, and was abundant throughout the lake in 1956. During the early 1960's the adult population more than doubled each year. Obviously this rate of increase could not continue because each new hatch of young encountered an increasingly greater population density and more competition for food and space. Data on age composition indicate that a decreasing percentage of young survived to become adults as the population increased. As this trend continued to a point where the number of adults was so great that it became very difficult for young to survive, the number of young reaching adulthood started to decrease and the population reached a peak. Evidence indicates that the population had reached this point during 1966–67.

Influence All Species

Because the alewife occupies various sections of the lake in dense schools during different seasons, it has influenced all other species of the lake. In midwinter the adult alewives are densely concentrated on the bottom in the deepest areas where they seek the warmest waters. This area was once occupied by the kiyi (*Leucichthys kiyi*), a chub that lived all year in the deepest area of the lake. The kiyi was very abundant as recently as 1954–55, but it had become greatly reduced by 1960–61, and was rare by 1964.

In late winter and early spring the alewives move toward shore in dense schools that pass through the region occupied by a small chub called the bloater (*Leucichthys hoyi*). This region is also occupied by the alewife in the fall as it returns to deep water. The bloaters increased greatly during the 1950's after the sea lamprey eliminated the predatory lake trout and five larger competing species of chubs. The total abundance of all species of chubs did not appear to change during this period, but the number of bloaters has been decreasing sharply in the 1960's as alewives have become very abundant.

Spawn in Summer

During the late spring and summer the adult alewives are concentrated in the shallower areas where they spawn near shore and in rivers and bays during June and July. The lake herring *(Leucichthys artedi)* and the emerald shiner *(Notropis atherinoides)*, which previously were extremely abundant in the shallow areas and bays of the Great Lakes, decreased sharply in various areas as alewives were first becoming established and have been very scarce or absent since the alewife became abundant.

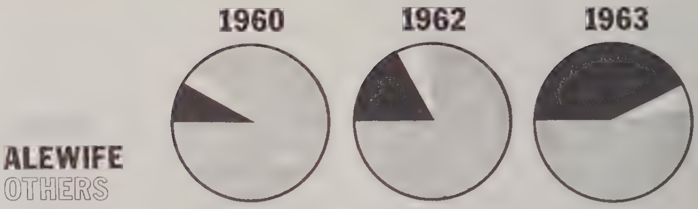
The yellow perch *(Perca flavescens)*, which occupies the inshore area, became more abundant as the alewives increased in Lake Michigan. The increase in abundance and resultant stimulation of fishing effort were reflected by an increasing catch of perch during the early 1960's that reached 5.8 million pounds in 1964. The increase in yellow perch may have resulted from the greater supply of food that the alewives provided for larger perch. As alewives became abundant they crowded the shore in dense schools during spring and summer and the yellow perch moved farther from shore. The concentration of alewives near shore, and the displacement of yellow perch, occurred during the spawning and hatching period of the yellow perch. As the alewives became very abundant during the early 1960's, recruitment of perch must have been reduced as the abundance of adult perch dropped sharply. This decrease was reflected by the sharp decline of the catch of yellow perch to 1.3 and 0.7 million pounds in 1965 and 1966, respectively.

The American smelt *(Osmerus mordax)*, which also occupied the inshore areas of the lake, declined sharply when alewife abundance increased. The smelt production in Lake Michigan declined from a peak of 9 million pounds in 1958 to about 1 million pounds a year since 1963. Because the American smelt is still abundant in Lake Ontario where the alewife has long been the dominant fish, it seems unlikely that smelt will be influenced as strongly by the alewife as were the chubs, lake herring, and emerald shiners, all of which are very scarce in Lake Ontario.

Competition Severe

During the fall and winter after hatching the young alewives occupy the middepths of the lake, where they remain until they are 2 years old. Then they move to the bottom. The midwater area has also been the zone occupied by the young of the lake herring, chubs, and American smelt during their first 2 years of life. Undoubtedly the competition between the young alewives and the young of the other species was severe as the alwives reached great numbers.

The occupation of various zones of the lake in different periods by dense congregations of alewives has greatly changed the utilization of the in-



THE WEIGHT OF ALEWIVES *in experimental trawl catches in Lake Michigan increased sharply from 8 per cent in 1960 to over 80 per cent in 1967.*

vertebrate food productivity by fish. The chubs, lake herring, emerald shiners, yellow perch, and American smelt all were very abundant species that occupied various sections of the lake and were major consumers of invertebrate food organisms in their respective areas throughout the entire year. Under present conditions in the summer when the alewife is concentrated inshore, the deepest water previously inhabited by the kiyi in great abundance is essentially unoccupied by an abundant species, and the productivity of invertebrate food there is incompletely used. Similar situations occur during other seasons when sections of the lake vacated by the alewives as they move from zone to zone are left with greatly reduced populations of the species that once occupied each section in high abundance throughout the year. As abundant as the alewife is, and despite its apparently intensive use of the invertebrate food of each zone of the lake during different seasons, it is very unlikely that the biomass represented by the alewife is equal to the total of all of the previously abundant species that it has displaced. The deepwater zone, which represents over 80 per cent of the area of the lake, is now occupied only sparsely by chubs during the main summer growing season.

Lake Ontario an Example

Lake Ontario may be an example of what can happen when one of the Great Lakes has long been dominated by the alewife. All abundant species from the deep water have become extremely scarce and one small species that lived near the bottom in the deepest water, the deepwater sculpin, *(Myoxocephalus thompsoni)* appears to be extinct. Lake herring and the several species of chubs are very rare. The smelt and yellow perch are common in shallower areas of the lakes but not abundant. A variety of other shallow-water species are even less common. Even the alewife, which is the most abundant fish in the lake, is not extremely abundant. Commercial catch records have shown a steady decline of the fish production of the lake yet its waters are rich in nutrients and abound with invertebrate fish-food organisms that seem to be incompletely used.

Rehabilitation of those Great Lakes dominated by the alewife to their former productivity, and the elimination of the unpleasant and costly problems caused by alewife dieoffs will require a drastic reduction of the alewife population and the reestablishment of a productive multiple species balance.

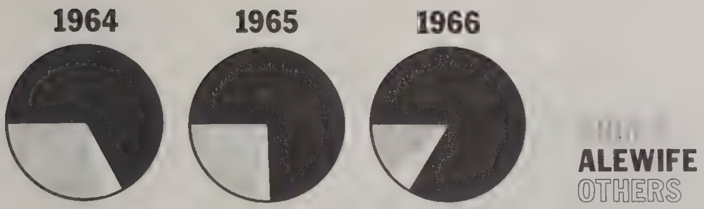
Alewife Fishery

An intensive commercial fishery for alewives in Lake Michigan that produced 29 million pounds in 1966 and reached about 40 million pounds in 1967 apparently has not greatly impeded the buildup of the alewife population. An even greater fishery may be able to reduce the alewife stocks because heavy exploitation has reduced stocks of close relatives of the alewives in the ocean—the Pacific sardine, menhaden, and Atlantic herring. It is doubtful if a fishery alone could reduce the abundance of alewives below the levels where they cause problems of dieoff or competition with other desirable species. An alewife industry requires a consistent supply of large quantities of fish that can be caught at low cost. Such production requirements could not be met at the alewife abundance before 1960, when the alewives constituted less than 10 percent of the fish in the lake. Yet they had already eliminated the kiyi, lake herring, and emerald shiner, and were causing distressing dieoffs each spring.

Predators Effective

Another means of reducing the alewife population is the establishment of large populations of predators that will feed on the alewife. Evidence that this measure could work can be seen in Lake Erie where the alewife has never become the dominant species, and in Lake Huron where the alewife was present since 1933 but did not start its population increase until the late 1940's after the predators had been eliminated by the sea lamprey. Its immediate increase after it was first found in Lake Michigan in 1949 was probably made possible by the lack of predators, and its failure to become more abundant in Lake Superior could be influenced in part by the continued presence of the lake trout and burbot.

Although the lake trout and burbot seem to have demonstrated their ability to keep the alewife population down, two new predators—the coho salmon *(Oncorhynchus kisutch)* and the chinook salmon *(Oncorhynchus tschawytscha)*—have been introduced recently. Experience gained from the first introduction of the coho salmon in Lake Michigan in 1966 indicates that it may be the most effective predator the Great Lakes has ever known —an effectiveness that is probably



very essential for survival in the wide expanses of its native Pacific Ocean. In Lake Michigan where there was a superabundance of alewives as food, reestablishment of the slow growing lake trout had been started in 1965 and offered little competition, and the sea lamprey had just been brought under control—the 660,000 coho salmon smolts planted in 1966 had a clear field. Over 30 per cent of the coho salmon were recovered before the end of 1967, and mature fish entering the spawning run weighed about 12 pounds. It has taken lake trout 11 years or longer to reach a similar size in the Great Lakes.

New Situation

It appears that the salmon may be much more capable of controlling the alewife than the native lake trout and burbot. There is, however, a great difference between the earlier situation in Lake Huron where the lake trout and burbot apparently kept the alewife from gaining a foothold during the 1930's and the present situation where the alewife not only dominates the lake but seemingly has lowered the overall fishery productivity by occupying the lake inefficiently after eliminating or greatly reducing all previously abundant prey species.

It is uncertain what will happen under this circumstance if the alewives are reduced greatly. Of the previously most abundant and productive native species, the lake herring and kiyi have been reduced to near extinction and the bloater has shown signs of extreme stress and possible genetic change that may inhibit its recovery. It cannot be anticipated which if any of these species might recover if the alewife is reduced. If they do not recover, the productivity of forage fish of the lake may be severely reduced. These species replaced by the alewife occupied some 80 to 90 per cent of the area of the lake and may have represented an equivalent proportion of the biomass of forage species under pre-alewife conditions. Even if the alewives continue at low abundance—below the level that causes troublesome dieoffs—the lake herring which previously had been the most abundant single species of the Great Lakes and the very abundant emerald shiner may not recover because these species disappeared when the alewives were scarcely abundant enough to be noticed.

The most critical requirement for rehabilitation of the Great Lakes is to make certain that other species fill in the void as the alewife is reduced. Reduction of the alewife should be slow enough to permit native species to recover if they can. If surveillance of the fish stocks shows that native species do not recover, steps must be taken swiftly to find and introduce suitable forage species that can occupy and thrive in abundance in the expansive deepwater areas of the Great Lakes.

Unstable System

The primary danger of rehabilitation of Lake Michigan is the extreme state of instability of its fishery system that has followed the complete collapse of a very stable system of interacting species which has evolved over thousands of years. The present system in which a single species, the alewife, makes up a major share of the forage fish of the lake is not stable. The instability is accentuated because the alewife is highly sensitive and not well adapted to its life in fresh water. Its abundance has fluctuated widely in the other Great Lakes where it has already reached its peak. Causes of these fluctuations are not known and cannot be anticipated. Overfishing or overpredation during the low cycle of a fluctuation could cause the alewife population to collapse, which could create a situation that might reduce severely even the minor forage species. A similar situation occurred when the predatory sea lamprey overpopulated the lakes by building up a superabundance when feeding on lush supplies of lake trout and burbot; then it destroyed the larger species of chubs and when these were gone it moved out of its preferred deepwater range and ravaged the whitefish *(Coregonus clupeaformis)*, walleyes *(Stizostedion vitreum)*, and suckers *(Catostomus* spp. and *Moxostoma* spp.) of the inshore areas and bays.

Research Essential

It is essential, therefore, that the rehabilitation of Lake Michigan and the other Great Lakes dominated by the alewife is accompanied by thorough research on all aspects of the fishery ecology. Changes in ecology, both desirable and undesirable, must be detected and interpreted quickly so that appropriate changes in management procedures can be implemented promptly to prevent the possibility of reversals or increased instability. Particular attention must be given to the possible population expansion of other undesirable species

Bureau of Commercial Fisheries

OVER THREE TONS *of alewives were taken in a single 15-minute drag in Chicago Harbor in May, 1967.*

as yet unnoticed or unknown. This kind of expansion can happen as experience has shown in the carp *(Cyprinus carpio)*, smelt, sea lamprey and alewife in past decades, and the recent takeover of Lake Erie by the freshwater drum *(Aplodinotus grunniens)*. Any such changes must be evaluated and dealt with expeditiously by redirecting the fisheries or by other appropriate means.

The prospects for the alewives of Lake Michigan in the near future are not clear. The extreme dieoff in 1967, which was the greatest known for any of the Great Lakes, has reduced the population greatly but alewives continue to be extremely abundant. The abundance of adult alewives in the winter of 1967–68 is about the same as in the winter of 1964–65. When alewives moved to shore in the spring of 1965 they caved in the screens of the Chicago water intake for the first time. The spring dieoff in 1965 was extensive and severe throughout the lake. Thus, if the conditions that influence severity of the dieoff are similar in 1968, the problems caused by alewives should be about the same as they were in 1965.

The hatch of young alwives in 1967 was phenomenal and was equal to or better than the 1964 hatch that contributed most to the record of 1967 dieoff. The reduced number of adult alewives in the lake caused by the 1967 dieoff increases greatly the chance of survival of the large 1967 hatch. Two conditions are different, however—a major commercial fishery has developed, and the 1967 hatch will bear the principal brunt of predation from some 7 million lake trout that have been planted in the spring during 1965–68 and some 4.5 million coho and chinook salmon planted in 1967–68. If the young of the 1967 hatch do not show up in abundance in the fall of 1969 when they become adults, we will know that the alewife has met its Waterloo. The serious and delicate task of reestablishing a new and more productive species balance will have begun. Success of this task rests heavily on the shoulders and capabilities of the scientists and administrators responsible for Great Lakes research and management.

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PROCEEDINGS
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A NEW CLINGFISH, *TOMICODON RHABDOTUS* FAMILY GOBIESOCIDAE, FROM THE LESSER ANTILLES[1]

By William F. Smith-Vaniz
Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami, Florida

Collections of shore fishes by Victor G. Springer, obtained under the auspices of the Breden-Archbold-Smithsonian Biological Survey of Dominica, contained several undescribed species, among which is a distinctive new *Tomicodon.* The new species brings to 11 the total known in the genus and represents a second species from the Atlantic Ocean.

The following description is based on the uniform plan and sequence previously adopted for this order of fishes (Briggs, 1955). Methods and terminology also follow those described in that work. Measurements included in the description were taken by measuring individual body parts and arithmetically dividing the results into the standard length.

For the privilege of examing specimens in their care I thank Drs. Warren C. Freihofer, Stanford University, C. Richard Robins, Institute of Marine Sciences, University of Miami, and Ernest A. Lachner and Victor G. Springer, United States National Museum (USNM).

Tomicodon rhabdotus new species

Fig. 1

Holotype: USNM 201804, 38.4 mm standard length (SL), collected just north of Bibay River, Bout Sable Bay, Dominica, bottom black sand and few rocks, 0–2½ ft., 13 November 1964, by V. G. Springer, R. H. Reckeweg, and P. Spangler (VGS 64–26).

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[1] Contribution No. 74, Tropical Atlantic Biological Laboratory, Bureau of Commercial Fisheries, Miami, Florida 33149 and Contribution No. 971, Institute of Marine Sciences, University of Miami, Miami Florida, 33149.

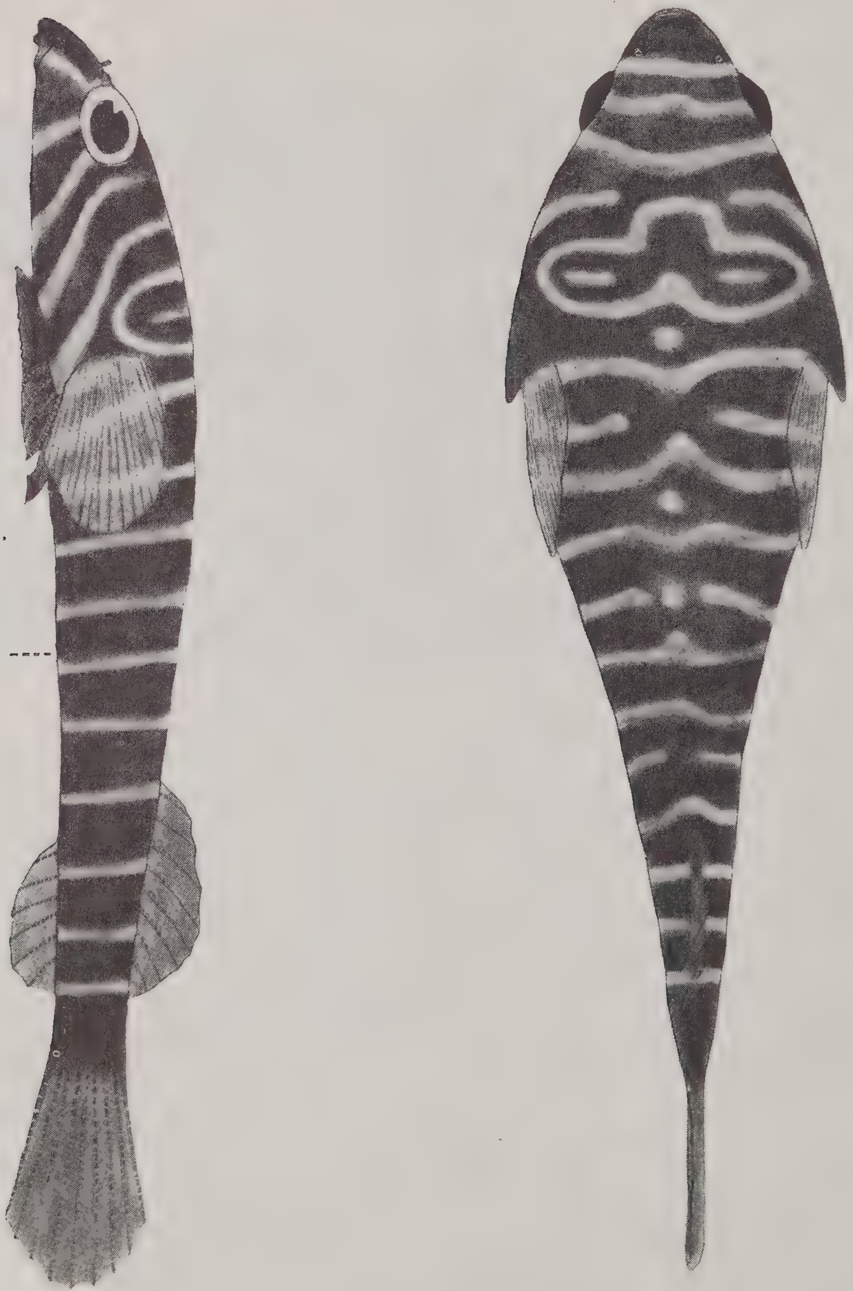

Fig. 1. *Tomicodon rhabdotus.* USNM 199561; paratype; 18.7 mm SL. (see text for data). A. Dorsal view. B. Lateral view.

Table 1. Comparison of three species of *Tomicodon*.

Character	*T. rhabdotus*	*T. humeralis*	*T. f. fasciatus*
Pectoral rays	18 (17 or 18)	18 (17 to 19)	21 (20 to 22)
Vertebrae	14 + 14 or 15 = 28 or 29 (usually 29)	14 or 15 (usually 15) + 14 to 17 = 29 to 32 (usually 30)	14 or 15 (usually 15) + 16 to 23 = 31 to 38 (usually 32)
Caudal rays	8	10 (9 or 10)	8
Dermal flap	large, height about 2 times diameter of anterior nostril	small, height usually less than diameter of anterior nostril	small, greatest height not exceeding diameter of anterior nostril
Position of anus	slightly closer to margin of disc than to anal fin origin	much closer to anal fin origin than to margin of disc	slightly closer to anal fin origin than to margin of disc
Pigmentation of sides	series of narrow pale vertical stripes against dark background	series of narrow pale diagonal stripes against dark background	series of heavy dark bars which extend partially to ventral surface against pale background

TABLE 2. Measurements of the holotype and two paratypes of *Tomicodon rhabdotus* (in thousandths of standard length).

	Holotype USNM 201804	Paratype USNM 199561	Paratype USNM 199560
Standard length (mm.)	38.4	18.7	15.9
Greatest body depth	126	126	107
Caudal peduncle depth	073	072	072
Caudal peduncle length	095	091	084
Head length	355	396	404
Head width	302	333	333
Snout length	094	086	075
Eye diameter	057	083	087
Bony interorbital	079	076	073
Dorsal-caudal length	284	259	248
Pectoral fin length	133	144	155
Postdorsal-caudal length	090	083	082
Disc length	293	297	309

Paratypes: USNM 199560, one specimen 15.9 mm SL, just north of Rav Anse Cola River and a little south of Colihaut, Dominica, bottom algal-covered rocks and barren boulders, 0–20 ft., 31 October 1964, V. G. Springer and R. H. Reckeweg (VGS 64–14). USNM 199561, one specimen 18.7 mm SL, Grand Bay, just south of Stowe, Dominica, bottom rocks and boulders, 0–15 ft., 2 November 1964, V. G. Springer and R. H. Reckeweg (VGS 64–16).

Diagnosis: A medium-sized *Tomicodon* with 5 pairs of trifid incisors in upper jaw and 4 pairs in lower jaw. Anus slightly closer to posterior margin of disc than to anal fin origin. Dermal flap extending from margin of anterior nostril comparatively large, simple, and broad at distal end; its height equal to or greater than distance between anterior and posterior nostrils. Distinctive pattern of narrow, pale, vertical stripes on posterior half of sides of body. Dorsal rays 9, anal rays 6, pectoral rays 18 (17 or 18), and caudal rays 8. Vertebrae $14 + 14$ or $15 = 28$ or 29, including hypural.

Description: Body moderately compressed, depth 7.9–9.3 in SL. Caudal peduncle short, least depth 1.2–1.5 in length. Head depressed, length 2.5–2.8 and width 3.0–3.3 in SL. Snout moderately shallow with a rounded outline, 3.8–5.4 in head length. Teeth in front of upper jaw consist of 5 pairs of trifid incisors in all specimens, followed on each side by 2 (1 or 2) well-developed canines. Lower jaw with 4 pairs of trifid incisors in all specimens, followed on each side by 3 (2 or 3) well-developed canines.

Greatest diameter of eye 0.8–1.4 in bony interorbital width and 4.7–6.2 in head. Subopercular spine moderately developed, but hidden by

Table 3. Frequency distribution of vertebrae in three species of *Tomicodon.*

Species	28	29	30	31	32	33	34	35	36	37	38	No.	mean
T. rhabdotus	1	2										3	28.66
T. humeralis		11	54	12	1							78	30.08
T. f. fasciatus[1]				3	31	9			2	2	1	48	32.62

[1] Although several specimens of *T. fasciatus* exhibited unusually high vertebral counts, they appeared to be otherwise typical.

heavy skin of opercle region. Upper attachment of gill membrane opposite 5th (5–6) pectoral ray.

Dorsal-caudal distance may extend forward as far as the posterior margin of pectoral fin. Postdorsal-caudal distance 1.8–2.0 in dorsal length. Disc length 3.2–3.4 in SL. Disc region A with 6–7 rows of flattened papillae across its width; 9–10 rows across width of disc region B.

Coloration: No color observations were made at the time of collection. Specimens examined shortly after being placed in isopropanol, exhibited a rich olive-green ground color. The light diagnostic markings (fig. 1) were pale yellow, perhaps as a result of fading. After several months in alcohol, the ground color faded to brown. Configuration of the pale body markings is nearly identical in all specimens; the markings were more conspicuous, however, in the two small paratypes which were noticeably darker than the holotype.

Etymology: From the Greek, *rhabdotus,* meaning striped.

Discussion: As indicated in Table 1, the new species is not closely related to *T. fasciatus* (Peters), the only species of the genus known previously from the Atlantic Ocean. Of the Eastern Pacific species of *Tomicodon, rhabdotus* is probably most closely related to *T. humeralis* (Gilbert), endemic to the Gulf of California. Although the two species are easily differentiated, they have in common low vertebral and pectoral-ray counts, and a high dorsal-ray count. Configuration of lateral markings is similar in the two species. The major difference is that in *rhabdotus* the lateral stripes are nearly vertical, whereas in *humeralis* they are diagonal.

The apparent restricted distribution of *Tomicodon rhabdotus* and the similarities it shares with *T. humeralis* suggest that it has only recently invaded the Atlantic Ocean. In contrast, the wide distribution and the occurrence of two forms, subspecifically distinct, indicate that *T. fasciatus* has long been established in the Atlantic.

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TRIAKIS FEHLMANNI, A NEW SHARK FROM THE COAST OF SOMALIA

By Stewart Springer
Bureau of Commercial Fisheries Ichthyological Laboratory
U. S. National Museum, Washington, D. C.

A 46-cm adult female specimen of a remarkable new shark (Triakidae) collected off the coast of Somalia during the International Indian Ocean Expedition (I.I.O.E.) is described here and assigned to the genus *Triakis.*

Smith (1957) referred to species grouped by Bigelow and Schroeder (1948) in *Triakis* as an uneasy assemblage. This is an understatement in view of the remarkable diversity in the group noted by Smith (1957), Kato (1968), and L. J. V. Compagno (in correspondence). The addition of the new species places more strain on currently used definitions of genera and families of galeoid sharks and emphasizes the need for review of characters that are traditional for their recognition. For the purposes of this description, however, I follow Bigelow and Schroeder (1948) with some exceptions and make only those amendments required by the addition of the new species.

The family Triakidae and the genus *Triakis* as provisionally redefined here includes species with functional gill-rakers as well as species without them, and also includes species with as many as 7 cusps on lower jaw teeth toward the angles of the jaws. The gill-rakers of the new species are not homologous with denticle-derived structures in *Cetorhinus* and *Rhincodon* that Bigelow and Schroeder evidently had in mind as typical shark gill-rakers, but externally resemble those found in some squaloid species (see Daniel, 1934, p. 154, fig. 147). In the new species the structures are skin-covered, springy projections extending and interdigitating across the inner branchial apertures from both sides of the branchial bars. They are short but presumably serve to make the branchial basket more effective as a strainer of small food particles. Structures of this kind are present but developed to varying degrees in several small triakid and scyliorhinid species; in *Triakis barbouri* (Triakidae) and in *Halaelurus canescens* (Scyliorhinidae), for example, they are nearly as strong as in the new species, whereas, in *Cephalurus* (Scyliorhinidae) they appear as mere mounds of tissue or as short villi. These structures are absent from the various species of *Mustelus* and from *T. scyllia, T. semifasciata*, and *T. maculata*. Teeth toward the angles of the lower jaw of the new species have seven or more cusps, a condition that it shares with *T. attenuata*.

The new species is named in recognition of the important contributions of Dr. H. Adair Fehlmann in setting high standards for field treatment of shark specimens collected for study.

Triakis fehlmanni new species
(Figs. 1, 2, 3, 4, and 5C)

Holotype: A 46-cm sexually mature female, U.S.N.M. 202969, collected on I.I.O.E. cruise 9 of the R/V *Anton Bruun* at station 463, 17 December 1964, in a trawl dragged at a depth from 70 to 170 m at 11° 24′ North Latitude, 51° 35′ East Longitude, southwest of Cape Guardafui, Somalia.

Material examined: the holotype is the only specimen of the species known. It was compared with examples of *Triakis scyllia* Müller and Henle, 1841; *T. semifasciata* Girard, 1854; *T. maculata* Kner and Steindachner, 1867; *T. barbouri* Bigelow and Schroeder, 1943; *T. (Neotriakis) sinuans* J. L. B. Smith, 1957; *T. (Eridacnis) radcliffei* H. M. Smith, 1913; *T. venusta* (= *Calliscyllium venustum* Tanaka 1912, probably also = *Proscyllium habereri* Hilgendorf, 1904); *T. henlei* Gill, 1862; and several species of *Mustelus*. I did not see specimens of *T. attenuata* Garrick, 1954 or *T. acutipinna* Kato, 1968, but both were given thorough and modern descriptions and present no difficulty in diagnosis. Specimens of *Hemitriakis leucoperiptera* Herre, 1923, were not available for comparison. I agree, however, with L. J. V. Compagno (in correspondence) that it cannot be placed in *Triakis*.

Diagnosis: The distinctive color pattern of this species sets it apart from all other sharks. It is also unique among galeoid sharks in having

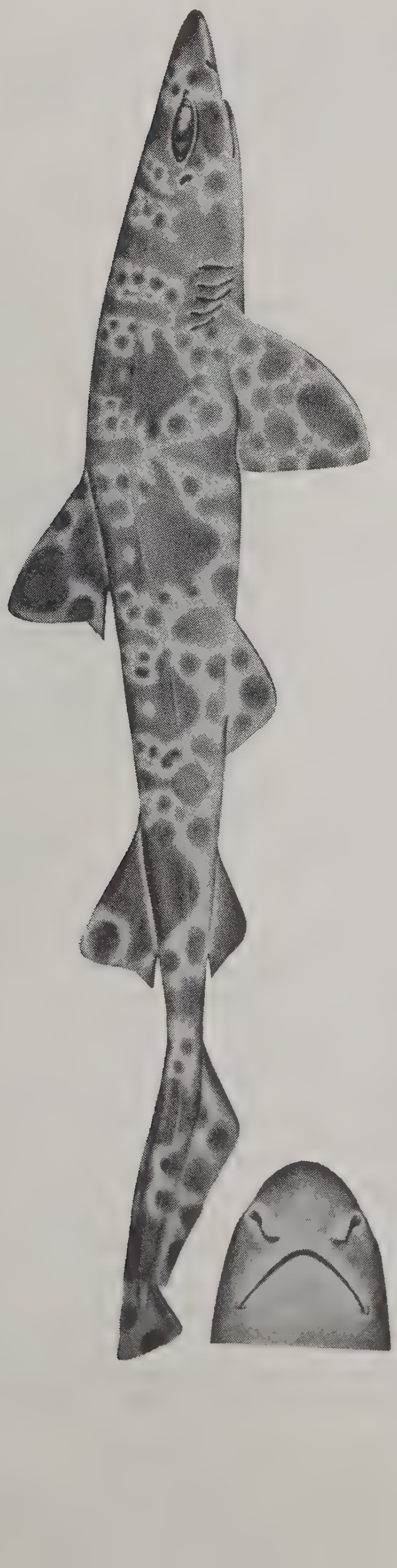

FIG. 1. *Triakis fehlmanni*, new species, 46-cm female holotype. Drawing by Mary H. Wagner.

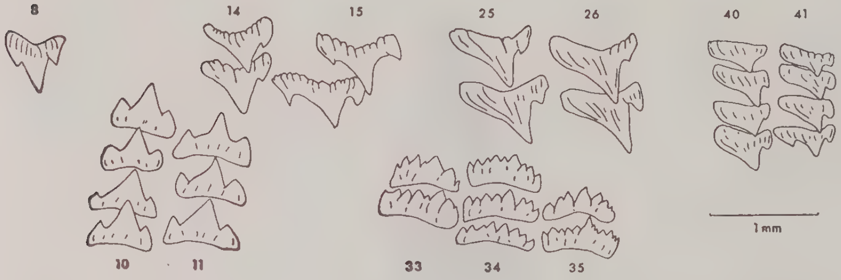

FIG. 2. Camera lucida outlines of teeth of *Triakis fehlmanni* new species. Upper row, teeth from upper left jaw (numbers below tooth groups indicate number of tooth row counting from symphysis). Lower row, teeth from lower left jaw.

large inner and outer nasal flaps that are irregularly scalloped along their posterior margins.

T. fehlmanni resembles *T. scyllia, T. semifasciata, T. maculata,* and *T. acutipinnis* in general body form, fin position, and fin shape as viewed laterally, although the lower caudal lobe is not produced to the extent that it is in adults of some of these species. It differs from them in that it has a wider and more flattened head, a wider mouth with smaller and more numerous teeth, very short labial furrows, short but functional interdigitating gill-rakers, and a comparatively shallow subocular gutter fully lined with denticles instead of a deep and incompletely denticle-lined subocular pouch.

The similarity of the new species to the various species of *Mustelus* in body form, and in fin shape and position is also striking. Furthermore, the large number of tooth rows in *T. fehlmanni* and their pattern of tooth arrangement in quincunx with more functional rows near the symphysis of the lower jaw are similar to that in species of *Mustelus. T. fehlmanni* differs from species of *Mustelus* in that it has multicuspid and sharp-pointed teeth, a wider head and mouth, shorter labial furrows, and functional interdigitating gill-rakers.

The gill-rakers of *T. fehlmanni* have slender, pointed tips but arise from wide bases, those of the anterior rim of one gill arch alternating in position with those of the posterior rim of the adjacent gill arch. Furthermore, they are as large and numerous around the anterior gill apertures as around the posterior ones and are also present around the spiracular pocket. In contrast, the gill-rakers of squaloid sharks, although proportionally higher, arise from slender bases chiefly on the posterior rims of gill arches and, if present, are usually larger on the posterior arches or are confined to posterior arches as in some species of *Centrophorus.* No observations were made on the comparative histology of the gill-rakers of galeoid and squaloid sharks.

Triakis barbouri, T. sinuans, T. radcliffei and *T. venusta* have the

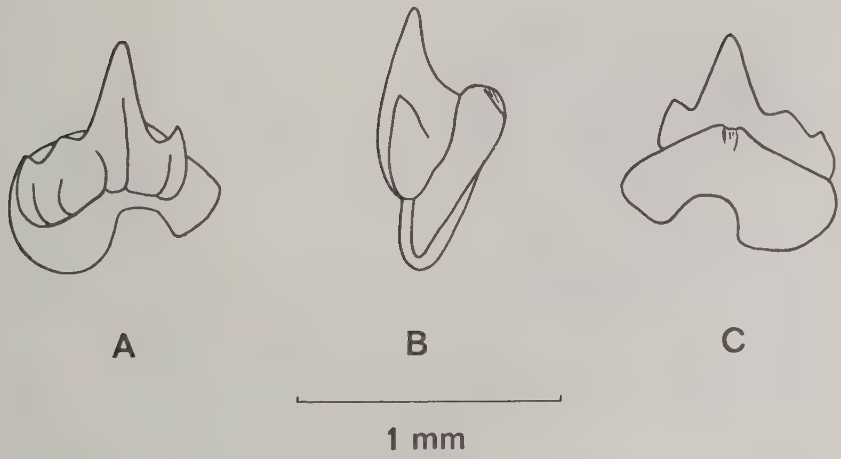

FIG. 3. Camera lucida outlines of 10th upper jaw tooth counting from symphysis. A—anterior face. B—lateral aspect. C—posterior aspect.

anal fin slightly in advance or nearly under the origin of the second dorsal fin, whereas in *T. fehlmanni* the anal origin is appreciably posterior to the origin of the second dorsal.

Triakis fehlmanni may be distinguished easily by its color and comparatively short body, from the plain-colored and elongate *T. attenuata*. *T. fehlmanni* and *T. attenuata* are similar in that both have broad, flattened heads, wide mouths with short labial furrows, and numerous small teeth of somewhat similar shape arranged in similar patterns. In both species the origin of the anal fin is posterior to the origin of the second dorsal.

Description: Proportional dimensions of holotype are in percentages of total length except as indicated. Measurements were made as outlined in Bigelow and Schroeder (1948).

Tip of snout to: front of mouth, 6.5; eye, 5.9; spiracle, 11.5; first gill opening, 18.3; fifth gill opening, 22.8; origin pectoral, 22.0; origin first dorsal, 33.7; origin pelvics, 43.0; origin second dorsal, 58.9; origin anal, 61.7; origin upper caudal lobe 76.5; anterior end cloacal opening, 45.9.

Greatest width of: head, 13.7; trunk at pectorals, 10.0; trunk at pelvics, 6.3; trunk at origin caudal 2.0.

Greatest height of: head at spiracles, 7.2; trunk at pectorals, 10.0; trunk at pelvics, 8.3; trunk at origin caudal 3.0.

Eyes: horizontal diameter, 4.3; vertical diameter 1.7; distance between supraorbital rims, 3.9.

Spiracles: greatest diameter, 0.9; least distance from eye, 1.2; distance between, 9.1.

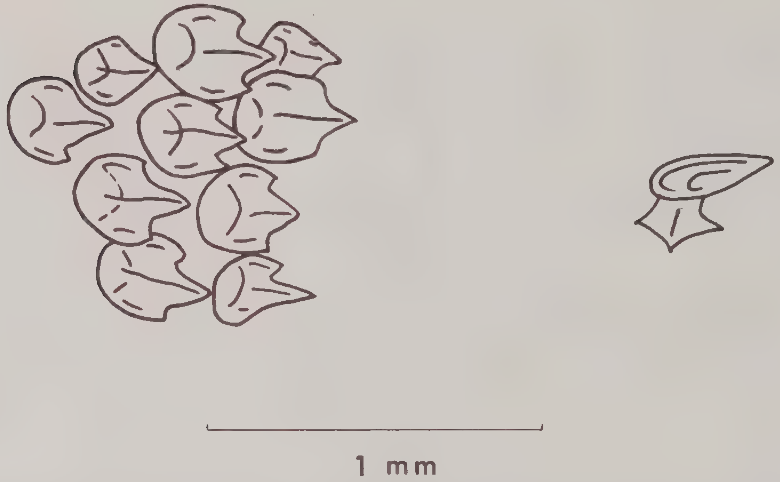

FIG. 4. Camera lucida outlines of dermal denticles from shoulder area of *Triakis fehlmanni* new species.

Mouth: width, 9.3; length, 3.9; length upper labial furrow, 0.2; length lower labial furrow, 1.1.

Nasal apertures: level of anterior ends to tip of snout, 3.7; level of posterior ends to front of mouth, 0.7; minimum distance between, 3.5; greatest length (diagonal), 3.3.

Gill slits: height of first 2.2; height of fifth, 2.0.

First dorsal fin: length base, 8.3; length posterior tip, 3.5; height, 7.2; length anterior margin, 9.8.

Second dorsal fin: length base, 9.3; length posterior tip, 2.8; height, 6.3; length anterior margin, 11.7.

Anal fin: length base, 7.0; length posterior tip, 2.6; height, 3.0; length anterior margin, 7.0.

Pectoral fins: width base, 5.0; length anterior margin, 13.9; greatest width, 10.4.

Pelvic fins: length (origin to rear tip), 9.8.

Caudal fin: upper margin, 23.0; anterior margin lower lobe, 8.9; tip to notch, 5.9.

Distance between fin bases: first to second dorsal, 17.8; pectoral to pelvic, 19.0; pelvic to anal, 11.7; anal to lower caudal, 6.5; second dorsal to upper caudal, 8.3.

Posterior tips of fins to fin origins: pectorals (appressed) to pelvics, 7.0; pelvics to anal, 8.3; anal to lower caudal, 4.1; second dorsal to upper caudal 5.4.

Teeth: upper, 86 rows; lower, 88 rows; width base, widest upper, 0.9 mm.; height, highest upper, 0.5 mm.; width, widest lower, 0.8 mm.; height, highest lower, 0.5 mm.

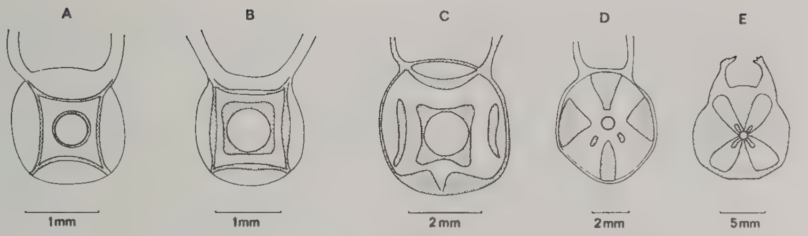

FIG. 5. Camera lucida outlines made from radiographs through the longitudinal axis of a single trunk vertebra to show calcification pattern. A—from *Eridacnis radcliffei*, a 25-cm female. B—from *Triakis barbouri*, a 29-cm female. C—from *T. fehlmanni* new species, type, a 46-cm female. D—from *T. semifasciata*, a 59-cm female. E—from *Mustelus canis*, an adult female about 150 cm (stippled and dark areas indicate calcification).

Vertebrae: total number, 137; number "monospondylous," 39; number precaudal, 90; number caudal, 47; A-value (see Springer and Garrick, 1964, p. 79), 128; B-value, 111; greatest diameter, 4.2 mm.

Gill-rakers: height of largest, 1.2 mm.; 6 or 7 on each side of ventral arms and 2 or 3 on each side of dorsal arms of gill bars 2, 3, and 4.

A small species; 46-cm holotype is sexually mature; head long, very wide, depressed; five gill slits, 4th over pectoral origin; abdominal body segment short, approximately circular in cross-section at pectoral level, trunk tapering toward tail, somewhat compressed posteriorly; no precaudal pits or keels; caudal axis slightly but definitely elevated; no nasal barbels or thickened areas on nasal flaps; nostrils not connected with mouth by groove; length caudal more than 2 times length first dorsal base; first dorsal base entirely in advance of origin pelvics.

Snout broadly rounded, slightly narrowed at nostrils, its length from front mouth about 0.7 times width mouth; large nasal apertures in posterior half snout, separated by about 0.5 times snout length; outer and inner nasal flaps large, their posterior borders in apposition and irregularly crenulate; pores of underside of snout moderately prominent, forming Y-shaped pattern in single row with base near front of mouth.

Eyes large, about 2 times as long as high, their lengths about half length of snout, situated well above rim of head, angle of view as much dorsal as lateral, with a strong but shallow and fully denticle-lined gutter below eye extending from anterior end of eye nearly to spiracle; supraocular crest present, not extended over orbit as a shelf; interorbital distance only about 55 percent of interocular distance; spiracle moderately large, its height about half height of eye, located immediately posterior to eye and separated from eye by a distance a little more than greatest diameter of spiracle.

Mouth very wide, its width more than 2 times its length, about equal to length of second dorsal base; lower jaw sharply arched at symphysis; labial furrows very short, length of lower labial furrow slightly less than greatest diameter of spiracle and about 5 times length of upper; inside of mouth light colored with one anterior row and 2 medial rows of low papillae; no oral denticles; branchial basket large, a series of springy, papilla-like gill rakers on both sides of each branchial bar interdigitating across internal branchial apertures; 6 or 7 gill rakers, some scarcely more than mounds of tissue, along each side of ventral section of complete gill bars, 3 along each side of each dorsal section. smaller numbers around spiracular pocket; branchial bars and internal surface of pharynx without denticles.

Teeth small, numerous (83/86 rows); those of central part of both jaws tricuspid, generally symmetrical, middle cusp much the longest, slender, erect, pointed; lateral cusps short, most teeth wider than high; series continuous across symphyses without marked change in tooth shape or size; anterior faces of central teeth of both jaws with a series of striations running from roots into enamel surfaces; the striations of upper laterals reaching nearly to tips, those of lower teeth short; central teeth of both jaws with posterior flange-like extension of roots (Fig. 3) surrounding nutrient canal. Upper teeth in 4 to 5 functional series; teeth tricuspid and nearly symmetrical in middle of jaw, generally lacking an accessory cusp on side toward symphysis and main cusp oblique from about 20th row (counting from symphysis) to jaw corners. Lower jaw teeth in 5 to 7 functional series; functional area broader at symphysis forming pavement-like occlusion surface of tricuspid symetrical teeth; teeth transitional at about 20th row to 5 to 7 or more cusped teeth, comb-like, cusps subequal, main cusp only slightly larger and higher than others and located asymmetrically as the 5th, 6th, or 7th cusp toward the jaw-corner side of each tooth.

Dermal denticles (Fig. 4) of shoulder area small, less than 0.5 mm, only a little longer than broad; closely imbricate with 3 posteriorly-directed short points, middle point longest; points little elevated, a moderately strong central ridge with a weaker ridge on each side; external surfaces uniformly covered, variation in denticle size and shape similar to that in lower galeoids—that is, ventral denticles generally without accessory points, ridges obsolete; denticle points somewhat longer toward tail; denticles of leading edges of fins and around apertures smaller, smoother, and rounder than on flanks. No caudal crest; skin relatively smooth to touch except when rubbed toward the head; color pattern produced by skin chromatophores; denticles uniformly semitransparent.

Pectorals broad, tips and inner corner broadly rounded, distal margins straight, distance from tips of appressed pectorals to origin pelvics about 1.5 times horizontal diameter of eye. Pelvics relatively small, their outer contours broadly rounded, posterior tips rounded and not attenuate; no apron connecting fins; origins slightly anterior to tip of first dorsal but posterior to end of first dorsal base. First dorsal origin about over free inner angle of pectorals, apex rounded, posterior point sharp but short; slightly higher but about equal to second dorsal in area. Distance between dorsal bases slightly less than distance from pectoral axilla to pelvic origin. A depression or trench in the skin extending between dorsal bases and continuing from second dorsal base to caudal origin. Shape of second dorsal similar to that of first but slightly lower, its base slightly longer; distance from its tip to origin upper caudal about 1.5 times horizontal diameter of eye; end of its base about over end of anal base; tip extending only slightly beyond anal tip. Anal about 0.5 times as high as dorsals, its base shorter, its origin posterior to second dorsal origin by distance about equal to vertical diameter of eye. Caudal slightly less than 0.25 times total length, strongly notched below near caudal tip; its lower anterior section not projecting as a definite lobe.

Vertebral column comparatively slender; greatest diameter of monospondylous vertebrae about 4.2 mm (about 6.7 mm in *T. semifasciata* of equal total length); transition from monospondyly to diplospondyly in pelvic region clearly marked, alternation of length of vertebrae not apparent. Pattern of vertebral calcification (see Fig. 5) intermediate in complexity between that of *Triakis barbouri* and *T. semifasciata.*

Visceral cavity short, its lining not pigmented; liver size moderate, 2 liver lobes well separated posteriorly, extending about 0.75 of distance to cloaca; intestinal valve a spiral with about 10 turns; one ovary and 2 oviducts functional; nidamental glands small as compared to those of most scyliorhinids such as *Galeus* of about equal total length. Holotype has, in each oviduct, one very thin-walled, transparent, 45-mm by 17 mm egg-case enclosing an amorphous mass of egg-yolk material (no embryos detected); single ovary appears to have much amorphous yolk material except for several spherical yolk masses about 7 mm in diameter. It is not clear from the condition of the specimen whether reproduction is oviparous or ovoviviparous.

The holotype observed a few months after formalin preservation was marked by a series of rich brown dorsal saddles interspersed by smaller brown markings of bars and round or ovoid spots of varying size on a ground color of light tan. Ventral surfaces were yellowish white with some indistinct spots on the lower sides of the pectorals and caudal trunk. Color changes after transfer to alcohol were not great.

Comments on natural history and relationships.

The stomach of the holotype contained only the partially digested cephalothorax of one unidentified crustacean. The upper portion of the valvular intestine contained some granular material (about 1 mm diameter), possibly incompletely digested invertebrate shells.

The combination of large mouth, small teeth, and a large branchial chamber with interdigitating gill-rakers suggests that this shark feeds on very small invertebrates. The presence or absence of gill-rakers has rarely been noted in descriptions of sharks except for the kinds of denticle-derived gill-rakers in the huge plankton-feeding whale sharks and basking sharks. To see gill-rakers in most sharks it is necessary to open the branchial chamber. This dissection is best accomplished by cutting preserved and well-hardened specimens through the angle of the jaws and gill arches on the right side back to the pelvic girdle. I recommend this procedure as standard, at least in first laboratory examination of a shark species. Even with unique specimens such as the type of *T. fehlmanni* no great harm is done and access is provided for the search for additional identification characters sorely needed by the shark taxonomist. A cut on the right side of the shark leaves intact the left side preferred by illustrators.

T. fehlmanni resembles various species of scyliorhinids in its basic color pattern, tooth shape, heterodonty, slender vertebral column, clear and abrupt transition from monospondyly to diplospondyly, prominent pore system on the ventral side of the snout, and degree of development of a subocular gutter, as well as in its size at maturity and in its scarcity from tropical continental shelf collections. All of these characters as represented in *T. fehlmanni* point up the difficulty in the separation of the families Scyliorhinidae and Triakidae. My own separation of the two families is arbitrary. In the Triakidae the first dorsal fin base is entirely in advance of the pelvic fins, whereas, in the Scyliorhinidae the first or in one species the only dorsal fin, has some part of its base over or posterior to the pelvic origin.

Tanaka (1915) reported that *Triakis venusta* (= *Calliscyllium venustum*; probably also = *Proscyllium habereri*) is oviparous and consequently should be placed in the Scyliorhinidae instead of in the Triakidae where it has been left by most authors. He evidently regarded the character of egg laying as of overriding importance. Cadenat (1959) reported, however, that of the two morphologically very similar species, *Galeus melastomus* and *G. polli*, one lays eggs and the other (*G. polli*) produces living young. By the arbitrary definition I have used, both *T. venusta* and *T. fehlmanni* definitely fall in the Triakidae as can easily be determined by external examination.

Several graded series of structural differences may be identified from the small, usually slope-dwelling and demersal scyliorhinids though the usually medium-size triakids that usually live in waters of the continental shelf to the generally large shallow-water or surface-dwelling carcharhinids. Among the differences are gradations from small to large size; increase in the amount of calcification and strength of the vertebral column; a shift from small multi-cusped teeth toward unicuspid teeth, blade-like in the upper jaw; a development of the nictitating lower eyelid through a series of stages accompanying loss of the spiracle; a change from egg-laying to the development of large young nourished in later stages of embryonic life by a pseudoplacenta;

a loss in the relative volume and perhaps also in complexity of the Ampullae of Lorenzini; and an increase in the length of the clasper-siphons accompanying a moderate lengthening of the claspers, a loss of clasper hooks or reduction of clasper spines; and a change in fin positions and shapes. Also, accompanying an adaptive radiation from the kind of demersal life that characterizes the scyliorhinids to the kind of life of the surface-dwelling carcharhinids, are improvements in locomotion through changes in fin shape and position and through the increased buoyancy provided by a relatively larger amount of liver oil.

Existing galeoid sharks provide a fine example of an evolutionary series from which general trends can be demonstrated. Unforunately, but as might be expected, the course of evolution of galeoids seems to have proceeded with shifts in direction and rate for different organ systems. The existing galeoids do not lend themselves to separation neatly into families either by groups of characters or by marked discontinuities in the degree of specialization of one particular character. Attempts to produce a phylogenetic classification through emphasis of one character over another breaks down as more species and specimens from the outer continental shelf and upper continental slopes become available. The vertebral calcification pattern as used by White (1937), for example, may be a better indicator of size at maturity or depth of habitat than of phylogeny.

T. fehlmanni has many characteristics in common with scyliorhinid species, perhaps more than with triakid species. My use of the position of the first dorsal fin as the primary character for the separation of members of the families Triakidae and the Scyliorhinidae has the practical advantage that fin position is easily determined on any specimen and that, among presently known species, variational overlaps are not known. So long as it is understood that galeoid families are grouped for convenience in discussion and are not separated by conspicuous gaps in character continuity no harm is done.

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THE OCEANS, AN OVERVIEW REGARDING THE COMMERCIAL UTILIZATION OF SPACE

Robert E. Stevenson

Reprinted from Advances in the Aeronautical Sciences,
vol. 23, 1968

MAPPING OF THE LAND FROM SPACE [*]

Frederick J. Doyle [+]

In spite of 50 years of aerial photographic mapping, the job of mapping the world is far from complete, and the rate of obsolescence of existing maps nearly equals the production of new maps. The development of space-borne camera systems provides the best hope of accomplishing the world's mapping requirements expeditiously and economically.

A 12-inch focal length, 9 x 14½ inch format, vertical camera, supported by 24 inch focal length high resolution cameras would permit accomplishments of the following map needs:

(1) Complete topographic mapping at all small and medium scales up to 1:250,000 for any area in in the world.
(2) Establishment of photogrammetric control adequate for map compilation at scales as large as 1:50,000 to 1:25,000.
(3) Rapid mosaics and planimetric map revision at scales up to 1:25,000.

Spacecraft lifetimes adequate to give four looks at all areas will provide nearly complete coverage despite cloud cover.

On a cost per square mile basis, space photography is more economic than airplane photography, but this economy is attainable only when very large areas are photographed.

For complete paper, see microfiche AAS 67-106.

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[*] Based on Preprint AAS 67-106

[+] Chief Scientist, Raytheon Company, Autometric Operation

THE OCEANS, AN OVERVIEW REGARDING THE COMMERCIAL UTILIZATION OF SPACE [*]

Robert E. Stevenson [+]

The advent of orbiting space flights has given oceanographers the opportunity of making a breakthrough in the problem of "food from the sea". The over-view now possible of the vast ocean areas of the world allows the examination of waters heretofore unexplored and the evaluation of dynamic ocean features on a "real time" basis.

Of the photographs taken by Gemini astronauts, 658 show earth features which are of significance to the problems of ocean-atmosphere-land relationships. The photographs were taken with a Hasselblad 70 mm. camera, modified by NASA for use in the cramped quarters of the spacecraft. Both 38 mm. and 80 mm. focal length lens cones were used and the film was aerial Ektachrome. The amazing number of useful photographs taken with the rather simple equipment is a great tribute to the ingenuity of all of the astronauts, and is a clear harbinger of the data to come from more sophisticated systems.

Analyses of the 70 mm. photography of the oceanic and coastal areas make clear four conclusions:

1. There is a lot of unfamiliar geography between 30°N. and 30°S.
2. Many ocean features can be seen which had been heretofore known only from

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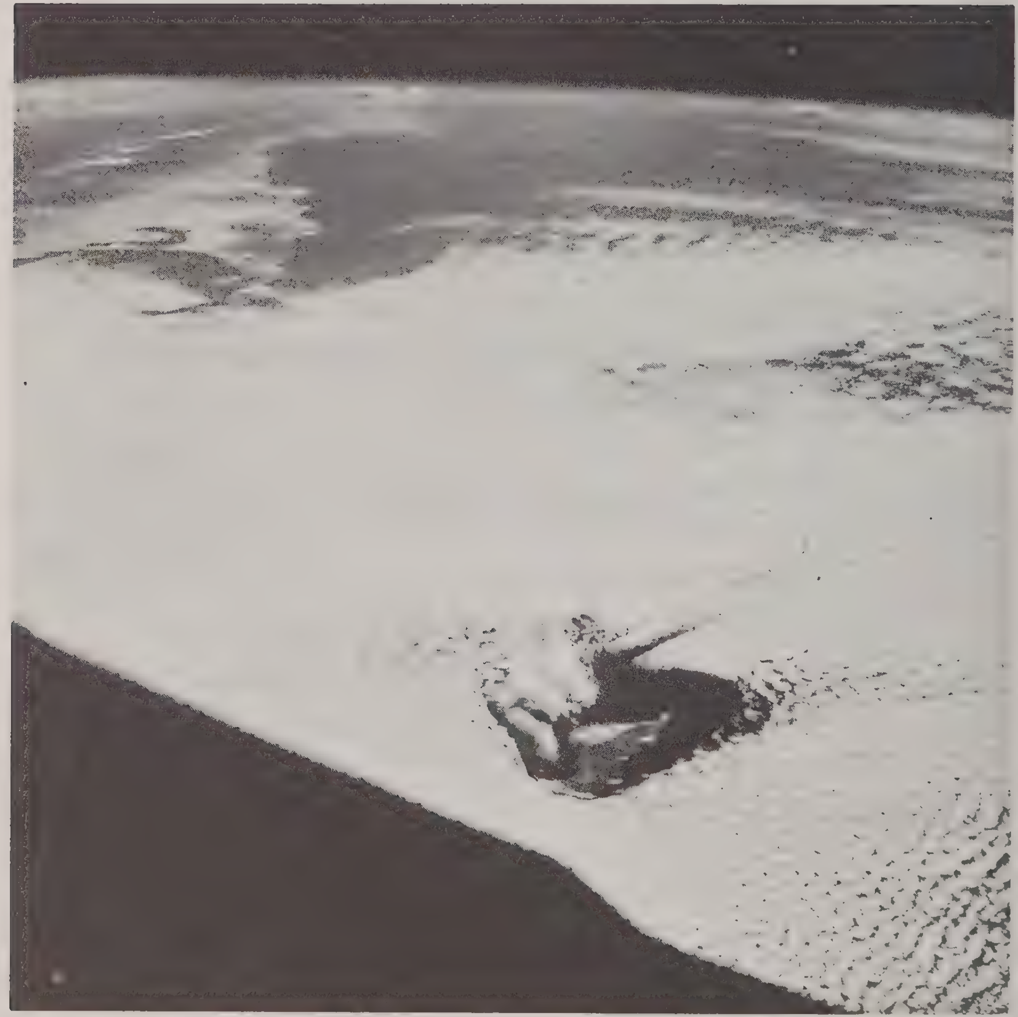
[*] Based on Preprint AAS 67-107

[+] Research Oceanographer, Bureau of Commercial Fisheries, Galveston, Texas theory and a few scattered data.

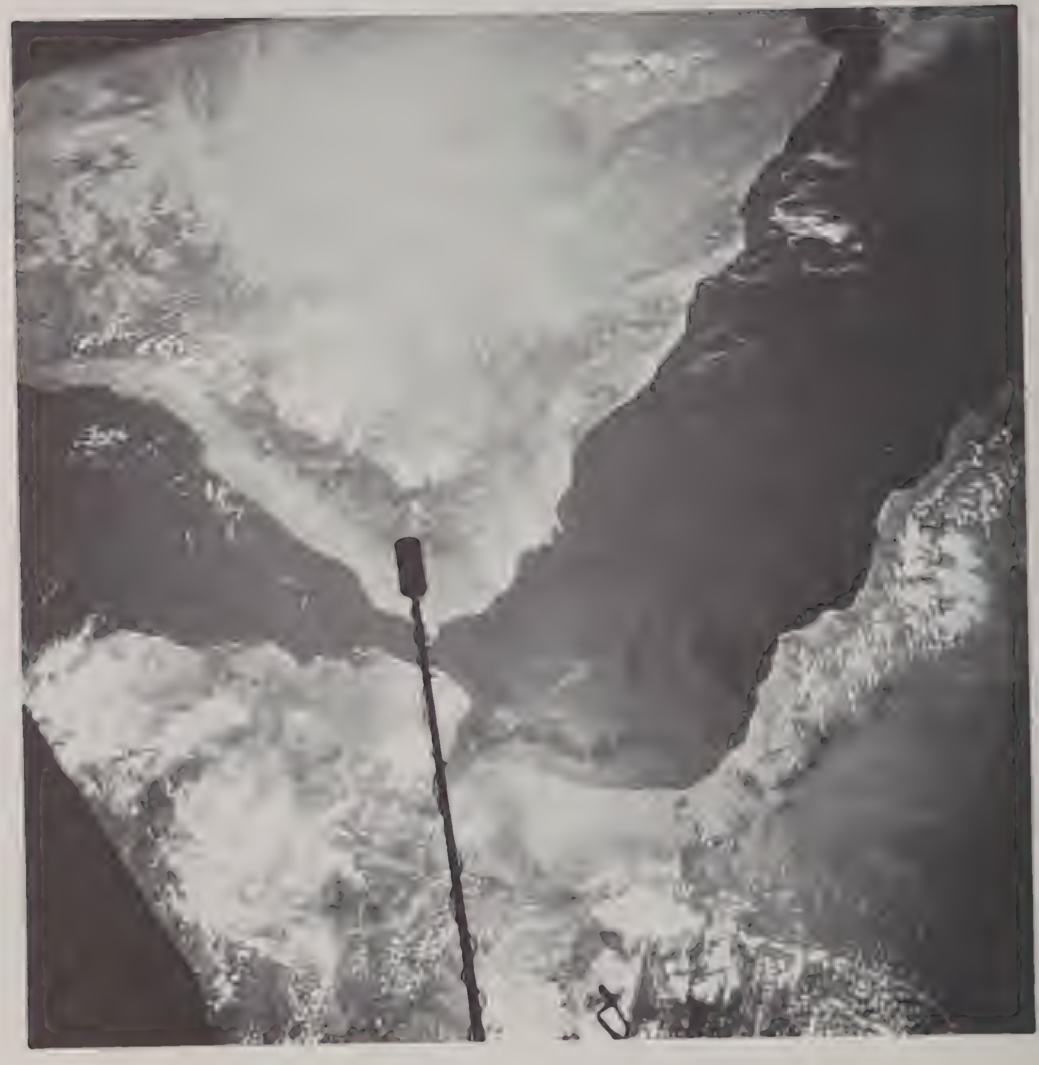
3. There are many structures in the surface layers of the sea which had not been known to exist that now can be seen from the vantage point of space.
4. We have much to learn about the oceans and seas of the world.

Four photographs are presented here. For the complete paper, see microfiche AAS 67-107.

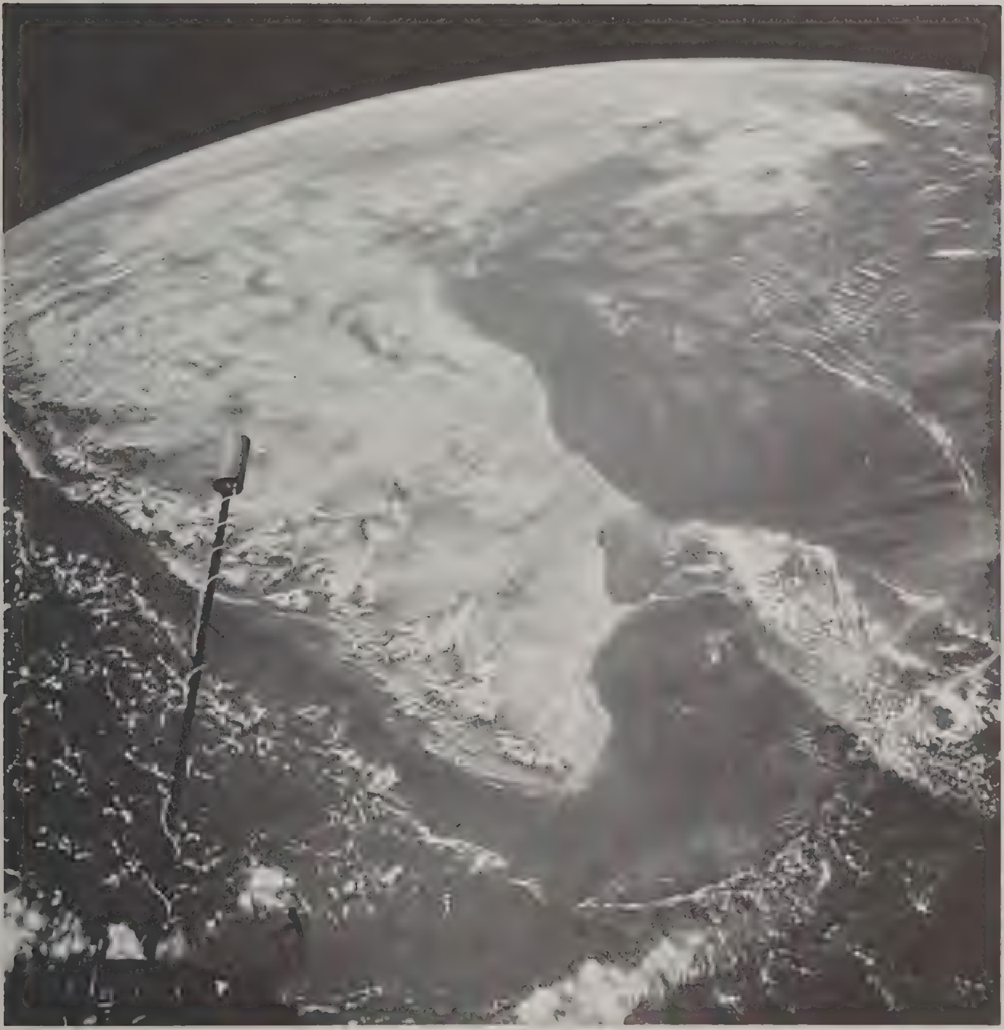


Photograph of Guadelupe Island, Baja, California, Mexico, and Vizcaino Bay taken August 21, 1965 from Gemini V.

Photograph of Southern Taiwan taken July 20, 1967 from Gemini X.



Photograph of Ethiopia, Somali, French Somaliland, Saudi Arabia, Yemen, South Arabia, the Red Sea, and the Gulf of Aden, taken September 14, 1966 from Gemini XI.



Photograph of India, Ceylon, Lacadive Islands, and the Bay of Bengal taken September 14, 1966 from Gemini XI.

SESSION 5E: EARTH AND ENVIRONMENTAL
SCIENCES -- EXPLORATION
PAPER 5E-4

THE VIEW OF THE OCEAN FROM SPACE[1]

Robert E. Stevenson
Bureau of Commercial Fisheries
Building 302, Fort Crockett
Galveston, Texas 77550

Photographs taken during the orbital flights of Gemini spacecraft have been evaluated to determine their utility for oceanographic research. Of about 1500 color photographs taken, 575 contain images which are uniquely significant to oceanography. Some features of the ocean that were previously unknown have been seen, measured, and interpreted. The existence of others, only suspected from severely inadequate data, has been confirmed.

From the evaluation, we have learned the size, kind, and variations of features at the sea surface that respond in a narrow portion of the electromagnetic wave spectrum. Furthermore, it is now known that emissivity in invisible parts of the spectrum is wholly suitable for remote sensing of the ocean. Microwave, infrared, and ultraviolet sensors, in addition to those responsive to visible wave lengths, clearly have applications in oceanographic research from space.

The ocean and atmosphere are dynamic. Air and water are in constant motion and interaction. Processes and movements vary in size from molecular to global. Because interactions of these processes are so complex, it is clear that totally practical rationalizations will not result from "classical" investigations. Yet, practical applications must be developed, for the ocean and atmosphere are part of man's environment. The cost of not adequately understanding the processes of these environments is enormous--not only in money, but in the lives lost through inadequate prediction and protection.

It seems reasonable, then, that man's hope of satisfactorily understanding the air-sea processes, and reaping the practical benefits therefrom, lies in the overall view of the oceans and the overlying atmosphere which is now possible from spacecraft.

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[1] Contribution No. 259, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

Reprinted from Synopses of papers, IEEE International Convention, New York, 1968.

[Reprint from JOURNAL OF GEOLOGICAL EDUCATION, Vol. XVI, No. 3, June, 1968]

View of the Earth from Space[1]

Robert E. Stevenson, Galveston, Texas[2]

The day is past when we merely talk or warn of the need for conservation and management of natural resources. Present requirements of undernourished and underpriviledged people are so great that if they are not met, political and economic, if not military, revolution will result. It is absolutely necessary, therefore, that the public recognize the relationships of the earth processes, forces and energies. Interaction of sea, air, and land must be better understood by everyone—otherwise, we will not be able to rationalize pollution control, efficient land use, and resource management, or realize the need for international natural resource treaties.

How do we make these relationships understandable?

A major problem for the student is the concept of magnitude. It is difficult for one to appreciate estuarine pollution without seeing an estuary. Nor can one realize the close relationship of coastal circulation to coastal geography without a concept of the magnitude of the interaction.

Furthermore, people must know the scale of the system to answer reliably such questions as: What is the most economic return from coastal utilization—housing, industry or natural fishery nursery grounds? What are the problems of thermal water pollution? Where is air pollution most likely to occur and what does the landscape-atmospheric reaction have to do with it? Without this knowledge, understanding is limited and answers are clearly provincial. Consequently, to ask legislators to vote on laws or regulations relating to these problems becomes useless.

Efficient management of the ocean, atmosphere and land resources must be established. It is the only solution to a peaceful, happy, growing society. To accomplish this goal, there must be an aware public.

A new tool is now available to education—the view of the earth from space. Student and teacher now have the opportunity to "see" the results of land-sea-air interactions on visual scales of sufficient magnitude to depict the significant major natural processes. Furthermore, the "view" is repetitive so that the changing forces, and reactions to them, can be followed. As a result, an understanding of the dependence of land features on air-sea reactions, of ocean motions on air-land interactions, and of atmospheric conditions on the land-sea relations can be greatly advanced.

BARS AND THE BAHAMA BANKS

An excellent example of land-sea-air interactions is provided by photographs of a portion of the Bahama

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[1] Contribution No. 269 of the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

[2] Research Oceanographer, Bureau of Commercial Fisheries.

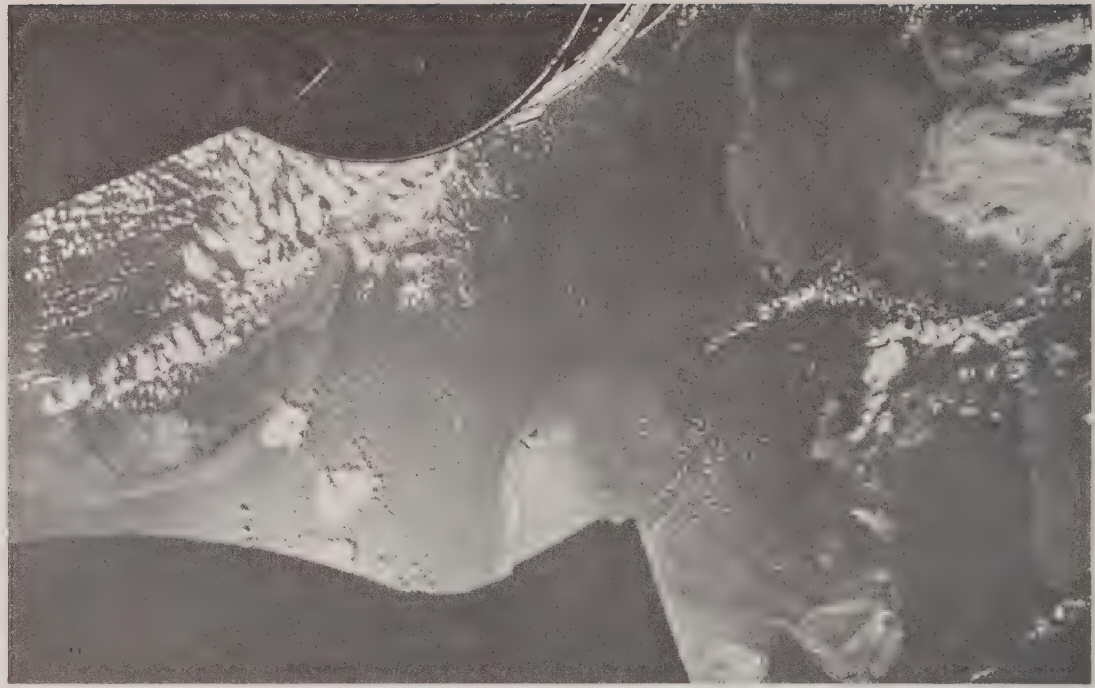

Figure 1. Southern Florida, Florida Keys, Florida Straits, and portions of the Bahama Islands and the Bahama Banks, Gemini flight XII, November 12, 1966, by astronauts Capt. James A. Lovell, Jr. and Lt. Col. Edwin E. Aldrin, Jr. NASA/MSC No. S66-62838.

Islands. In Figure 1, Florida Bay, the Florida Keys, and the Florida Straits can be seen beneath the open door of the spacecraft. Across the channel of the Florida Straits are the northern part of Greater Bahama Bank, the island of Bimini, the Berry Island group, the northern part of Andros Island, New Providence Island, and the city of Nassau. Under the nose of the Agena rocket are Grand Bahama Island, Little Bahama Bank, and the clouds overlying the waters of the Gulf Stream.

This photograph is particularly interesting because of the clear relationships of the shallow, calcareous sandbars which can be seen on the Great Bahama and Little Bahama Banks. Immediately to the south of Bimini Island are a number of large, more or less U-shaped bars that indicate the spillover of water onto the shallow platform of a portion of the Grand Bahama Banks. Similar spillover bars are present around the Berry Island group and the northern end of Andros Island (Figure 2). It is clear that in each area rising, flooding waters spill toward the central portion of Grand Bahama Bank. Near the top of the picture is a long sandbar where rising, flooding waters meet. On ebb tide, the waters recede into the channel between the Grand Bahama Bank and Grand Bahama Island to flow out into the Gulf Stream and then north into the Atlantic Ocean.

The flooding waters that form these large, magnificent bars are the result of great storm surges, coming primarily from the force of hurricane winds on the sea. Consequently, a sequence of interacting events exists which, when completed, leave their "mark" in the form of the flood and ebb spillover bars. The force of atmospheric winds on the sea necessary to produce the surging, rising waters that flood over the shoal Bahama Banks is easily imagined from the visual examination of sand bars 8 to 60 kilometers long.

DIAMONDS AND THE COASTLINE

Another sequence of natural events can be studied from the Gemini IV photograph of the Walvis Bay coast, Southwest Africa (Figure 3). This photograph of a cloud-free region is unusually detailed, for the photo resolution is the order of 30 meters or better. For example, the highway connecting Walvis Bay with Windhoek, as well as other small features such as the surf, can be seen clearly.

The area is largely a desert. Although most of southwest Africa consists of high plateau 1,000 meters or more in elevation, the coastal region, varying between 100 to 150 kilometers wide and about 500 kilometers long, is barren desert. None of the rivers within the limits of the photograph, nor for a considerable distance to the south, are perennial. The Swakop River is dry except for 1 or 2 months in the summer.

Because the region is a desert, with little or no surface runoff, turbid water normally would not be expected offshore. Careful examination of the photograph,

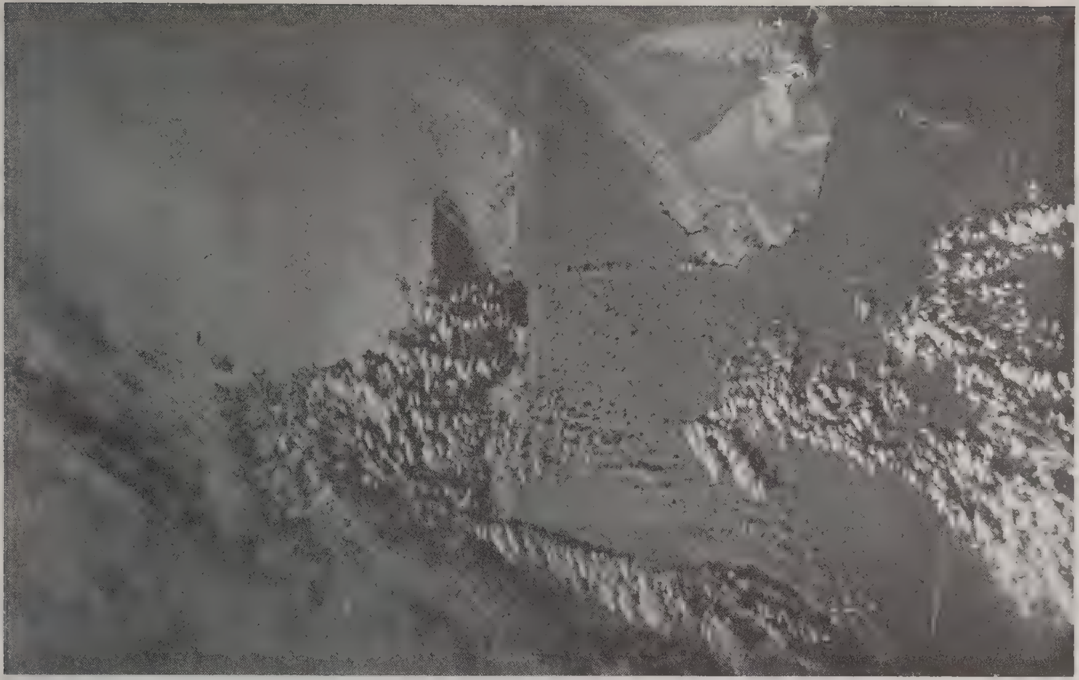

Figure 2. Northern end of Andros Island, Berry Islands, New Providence Island, and a portion of the Great Bahama Bank, Gemini flight VII, December 5, 1965, by astronauts Col. Frank Borman and Cdr. James A. Lovell, Jr. NASA/MSC No. S65-64956.

however, shows some evidence of turbidity. It is probably of biological origin.

An interesting observation is the distance that the average sea breeze penetrates inland. The ridge dunes dissipate rather abruptly near the coast in a confusion of small sand dunes. The landward edge of the disorganized dunes marks the penetration of the sea breezes.

The exceptionally dry climate is in response to the effects of the northward-flowing, cold Benguela Current. The air above the current is cooled so that little moisture is derived from the sea. Winds from the east are dry, having traveled over hundreds of kilometers of arid land.

Prevailing winds blowing towards the ocean produce the distinctive dune ridges that are oriented almost perpendicular to the direction of the wind. These long dunes are a result of winds blowing from nearly the same direction for centuries. Inland are the famous "diamond pipes" of South Africa. Diamonds weathered from the volcanic rocks have been, and are being, carried with the migrating sand to the coast. There, intense wave action from the South Atlantic Ocean has concentrated the diamonds on the shallow seafloor. There lie today the richest marine deposits known to man.

The white fringe along the shore, like a string of pearls, is caused by huge waves (typical of this shore) breaking nearly 200 meters from the beach. Rip currents about 1,000 meters long reflect in the sunlight and are the largest of the shoreline "pearls." Such intense surf action is normal and produces the great turbulence that transports the sand north along the coast and leaves the residual diamond concentration.

GREAT EDDIES AND THE TEXAS COAST

Systems of rip currents, reacting to the same causes as those formed in the surf along the southwest African coast, are formed over the Texas Shelf, but on a scale measured in tens of kilometers rather than meters. Examples are seen in the Gemini XII photograph of the Texas and Louisiana coast, taken by Lt. Col. Edwin E. Aldrin, Jr. on November 14, 1966 (Figure 4).

The skies were clear and the air was dry following the strong intrusion of continental air after a cold front crossed the coast on November 12. Winds were still blowing from the northeast on November 14, as can be noted from the seaward drift of smoke from a marsh fire along the Louisiana coast and the southwestward drift of industrial haze from the city of Houston.

In response to the brisk (22 kilometers/hour) northerly winds that had been blowing for two days, the coastal currents were flowing to the southwest. As during every strong northerly wind along these coasts, the water in the lagoons and estuaries was pushed into the Gulf of Mexico. Sediment-laden water (light) is seen

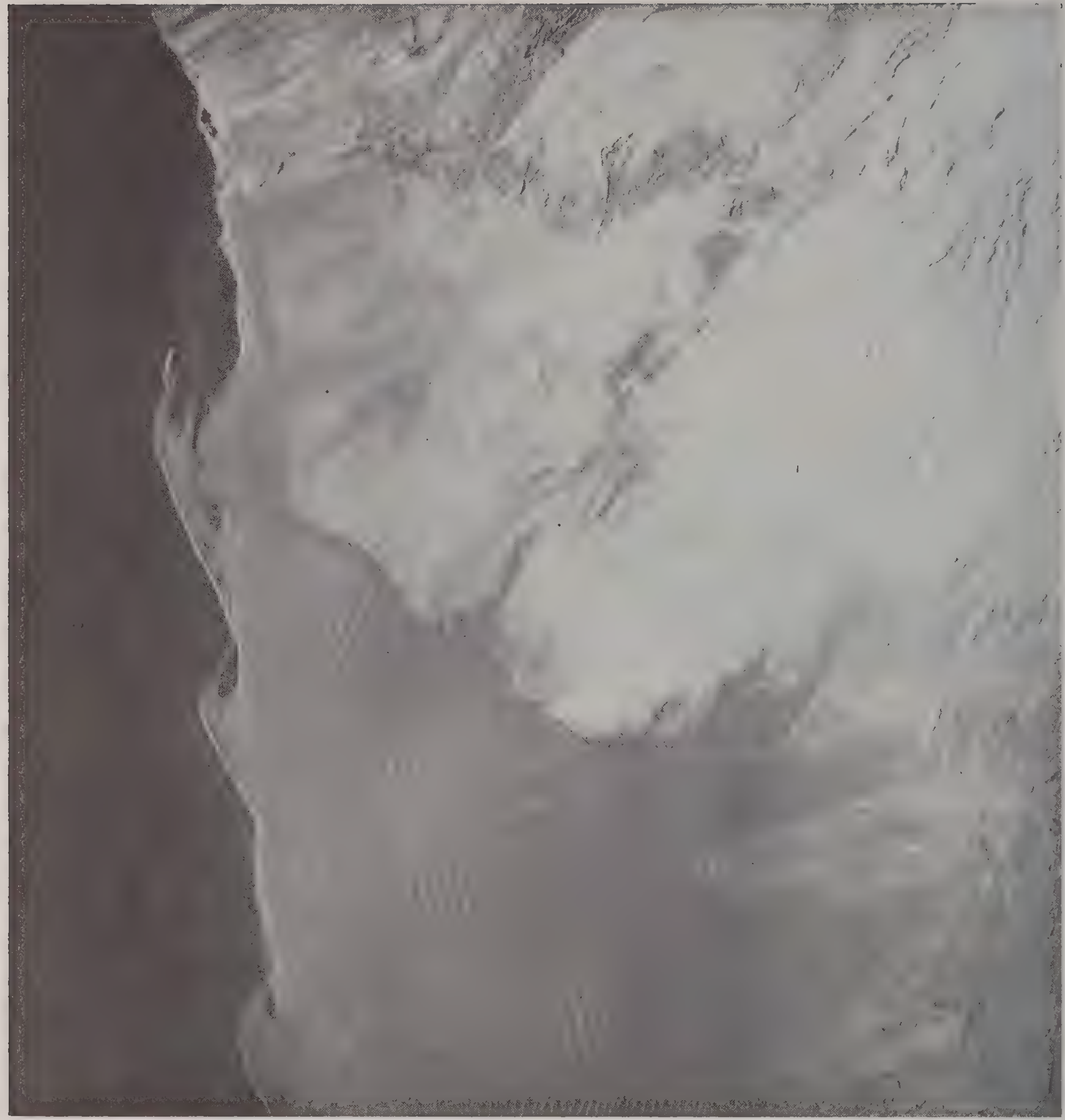

Figure 3. Southwest Africa, Port of Walvis Bay and the restricted diamond area, Gemini flight V, August 27, 1965, by astronauts Col. L. G. Cooper and Cdr. Charles Conrad, Jr. NASA/MSC No. S65-45524.

to be flowing out through Sabine Pass and between the jetties at Galveston Bay.

In Galveston Bay, the dark line is the dredged Houston Ship Channel and, in the northern part of the Bay, the light-colored streak extending from the mouth in the lower bay is extremely turbid water flowing from dredging operations.

The lighter coloring off the coast is turbid water spreading from the coastal lagoon complexes. An interference eddy has formed to the west of the Galveston jetties—the downstream side, here. Farther seaward, great eddies extend 45 to 150 kilometers from the coast over the shallow shelf (a depth of 100 meters is 200 kilometers from shore). These systems carry vast quantities of water from the nearshore shelf off Texas out into the Gulf of Mexico, thus relieving the build-up of sea level in the northwest Gulf much in the same manner that rip currents relieve the rising levels in the surf zone. The magnitude of the system in the northwest Gulf of Mexico is startling, for the seaward-flowing, turbulent currents must be permanent features of the waters over the Texas shelf although the position must

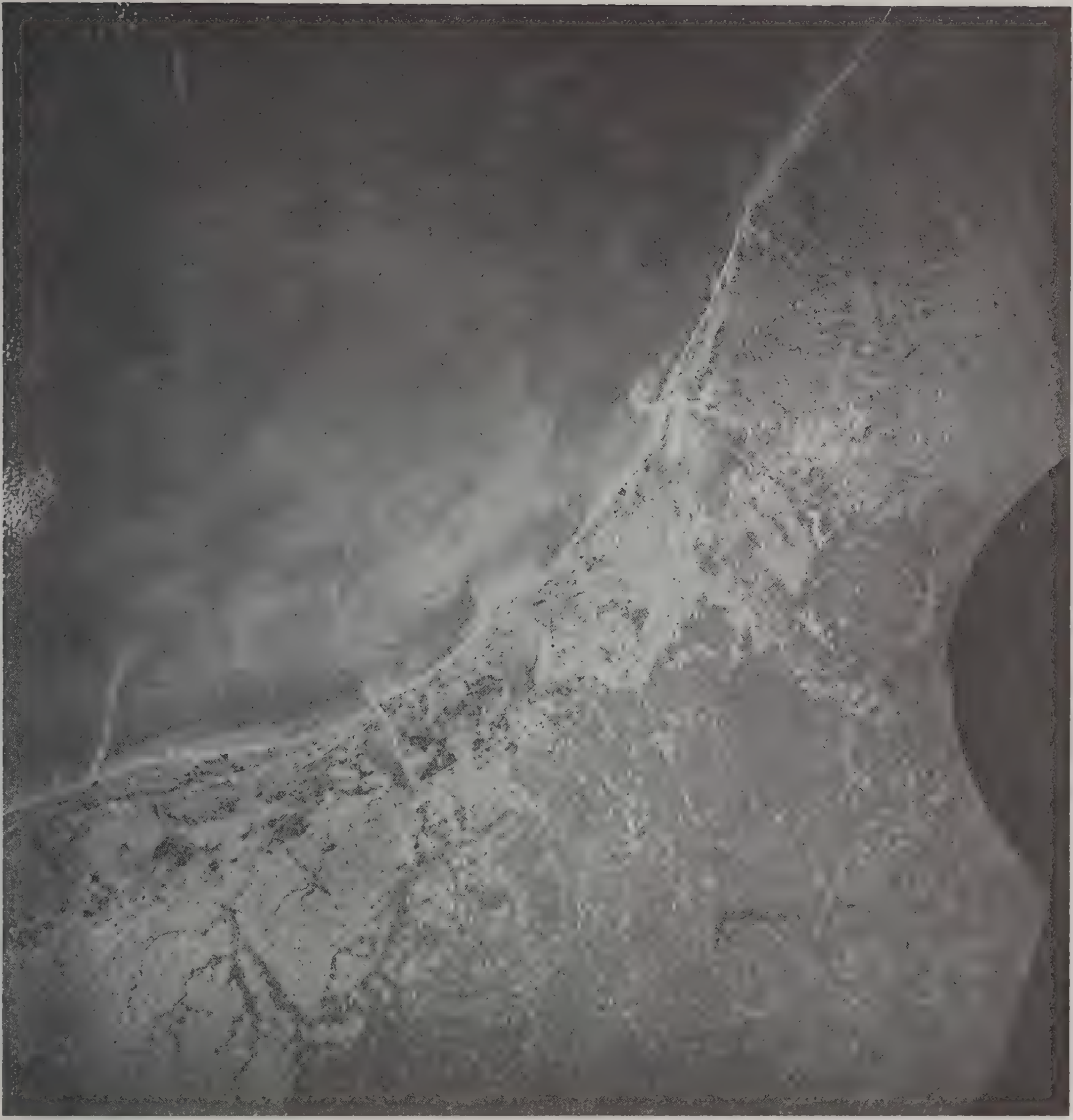

Figure 4. Texas and Louisiana coast, Gemini flight XII, November 14, 1966, by astronauts Capt. James A. Lovell, Jr. and Lt. Col. Edwin E. Aldrin, Jr. NASA/MSC No. S66-63184.

vary with the seasonal change of winds.

CLOUDS, WINDS AND CONVERGENCES

The distribution of turbid water can depict the relationships among coastal currents, tides, river discharge, and the lower atmosphere. A series of photographs taken by Gemini X astronauts along the coast of Surinam provides suitable examples.

Photographs off Surinam taken on July 21, 1966, show sediment-laden water poured out by the rivers and spread west along the shore. About 15 kilometers offshore the water turbidity indicated a flow to the east. The general current direction in these waters of the tropical Atlantic Ocean is to the west at velocities of 2 to 5 kilometers/hour. The distribution of the turbid water depicts, therefore, a current shear paralleling the coast.

The circumstances under which these currents and shear zones develop are not precisely known, and a considerable amount of detailed oceanographic research must be accomplished to interpret accurately the data derived from spacecraft.

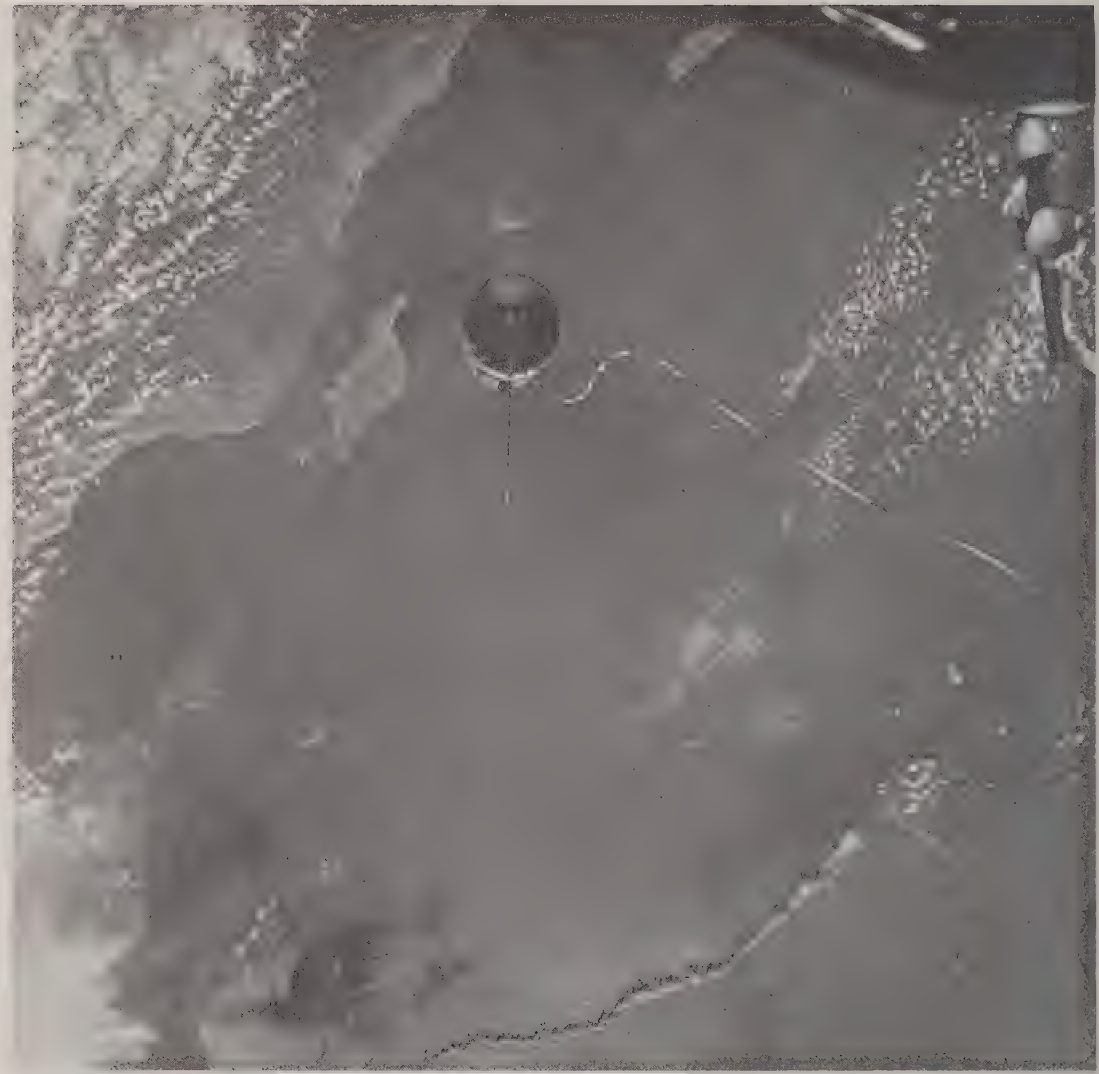

Figure 5. Southern Gulf of California, Baja California and the city of La Paz, Santa Cruz Island San Diego Island, San Jose Island, Espiritu Santo Island, and the northern end of the island of Cerralvo, Gemini flight XI, September 14, 1966, by astronauts Cdr. Charles Conrad, Jr. and Cdr. Richard F. Gordon, Jr. NASA/MSC No. S66-54761.

The suspected cause off the shores of Surinam is the tide. In these waters, the tide rises to the east and ebbs to the west. Because greatest velocities are next to the coast, the pattern observed was probably formed throughout a tide cycle. The muddy water showed the tide ebbing (at the time of the photograph studied) after a strong easterly flood 2 or 3 hours earlier. Lines of cumulus clouds extended northeastward and produced a convergence in the lower atmosphere—the marine friction layer. Air rising to form the cumulus was drawn in from the sides thereby producing the converging winds. These convergences were minor—not like those of a frontal system—and the winds and pressures developed would not appear on the usual synoptic weather map.

Under some conditions, the winds drawn into the atmospheric convergence move the surface waters to form a convergence in the sea. This kind of action occurred off Surinam on this day where the cloud lines were associated with the boundaries of turbid water.

A FISHERY RELATED TO THE CONFIGURATION OF A COASTLINE?

The southern Gulf of California with the city of La Paz on the left and the Mexican mainland on the right

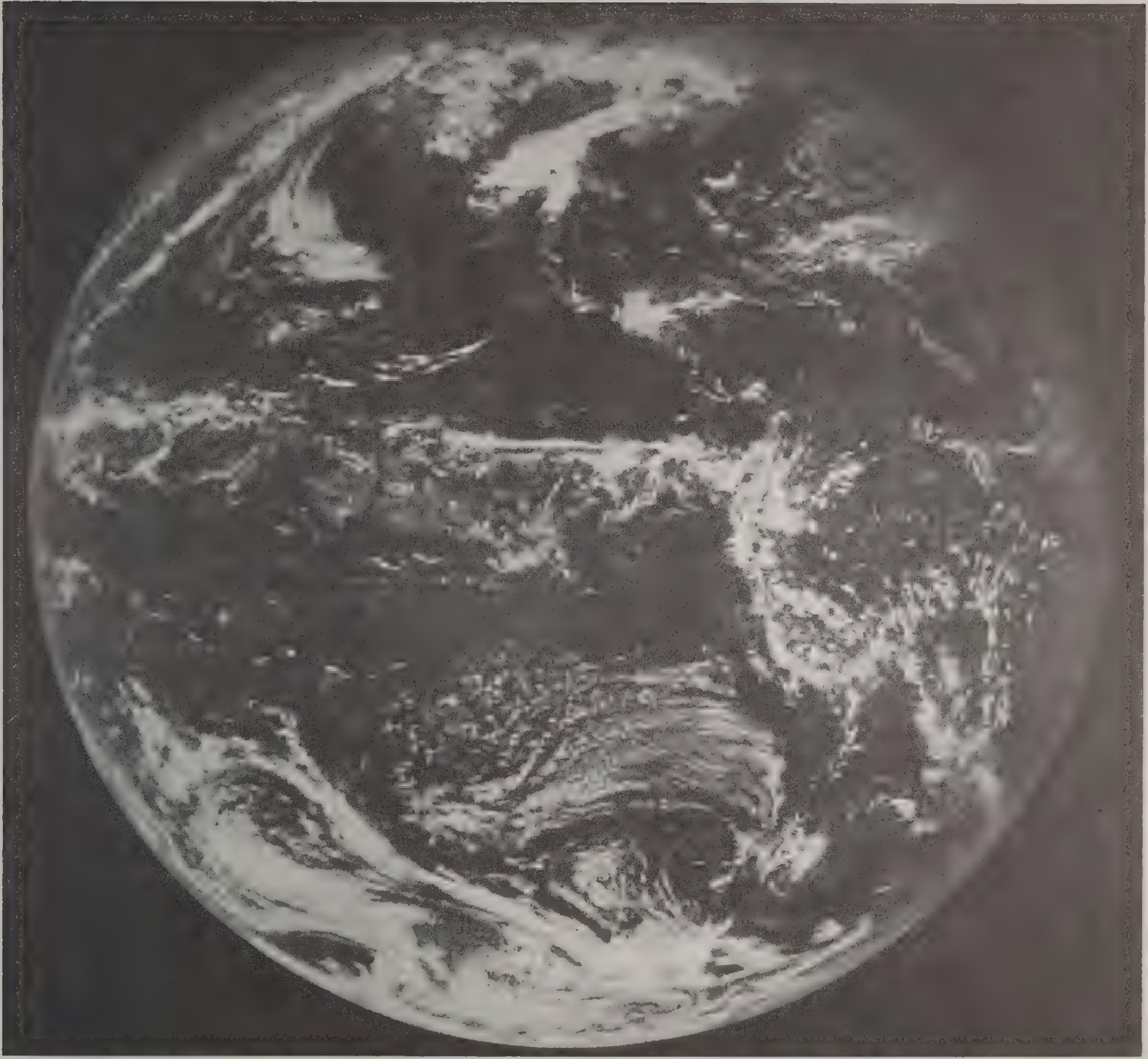

Figure 6. South America, Central America, Cuba, and portions of North America and the African continent, Application Technology Satellite III (ATS-III), January 18, 1968. NASA/MSC Color No. 193343Z.

was viewed by the Gemini XI astronauts September 14, 1966 (Figure 5). The edge of the sun's reflection is in the lower part of the photograph.

Of interest here are the slick in the strait between the La Paz coast of Baja California and the island of Cerralvo, the straight line of clouds to the north of the island of Cerralvo, and the large convergence under a long line of cumulus angling across the lagoons of the Mexican mainland coast. The slick pattern indicates water motion through the strait to the north, with a turbulent eddy north of Cerralvo. A convergent line in the water and in the overlying air lies to the northeast of the island.

Most impressive, however, is the convergence extending toward the Mexican mainland in a northeast-southwest direction. The flooding tide pours north into the Gulf of California from the Pacific Ocean and meets beneath the cumulus line those waters moving on the preceding ebb tide. The result is a strong convergence of waters with different temperatures marked by an overlying line of cumulus.

Winds on this day were easterly and hence the cumulus line formed on the warm side of the convergence. Flotsam, jetsam and food concentrated in the convergence provide excellent feeding for large fish such as marlin. The convergence line marks the great marlin fishing grounds off Baja California.

THE LONG RED SEA AND THE CURVED EARTH

The linear Red Sea lies in a graben produced by major rift faulting (cover photo). It is to this portion of the earth's crust that many advocates of continental drift point as evidence of continued rifting of large land masses. The features of mountains and coast are truly impressive examples of crustal faulting.

The long, straight, Red Sea Basin provides an unusual opportunity to identify with the curvature of the earth. Personal identification with the curved earth is difficult for anyone. We have known about the oblate spheroid from our youthful days and the stories of Columbus. Even so, and even with such phenomena as ships disappearing over the horizon, any "feeling" of a curved earth is rare. Consequently, photographs from space that show land features that can be related to a personal experience such as mountains, beaches, and rivers provide the perfect "identifier" of the round earth. This photograph, taken by Lt. Col. Edwin E. Aldrin, Jr. during the flight of Gemini XII, is one of the best "curved earth relators" that I have seen.

One may also understand from this photograph the reasons for the magnitude of air-sea interaction over the Red Sea—the merciless exposure to a cloudless atmosphere. The high salinity (40‰) and high temperatures (32° C.) of the water, the calcareous reefs (near the mouths of the Gulfs of Suez and Aqaba), the barren landscape, and the rigorous living conditions, can all be vividly imagined. Here too one can easily recognize the land modification and management practices that are so vital to the people in the Nile River Valley.

A NEW VIEW EVERY DAY

The view of the earth must be repetitive to follow the dynamic processes in the ocean and atmosphere. This repetitive view is easily available from satellites that are in a "parking orbit" (Figure 6). This view of the earth is from the color television camera on the Application Technology Satellite Number III (ATS-III) when it was situated over the Equator and at 84° W. longitude. A picture was transmitted every 20 minutes during the day so that the moving clouds and ocean currents could be plotted easily.

The picture reproduced in Figure 6 was taken at noon, local time, on January 18, 1968. Three major frontal systems can be seen in the northern hemisphere angling from northeast to southwest. The clouds of the Intertropical Convergence Zone extend east and west across the Pacific Ocean just north of the equator. Nearly clear skies lie over the warm equatorial current.

Our technology in satellite systems not only provides views of the magnitude seen from ATS-III, but also can provide photographic scales suitable to any user. Furthermore, such systems can readily bring this view and any other into any classroom in the world, whether it be the red brick buildings of Brooklyn, the stucco and redwood of southern California, or the thatched-roof huts in Samoa.

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Weltraum-Ozeanographie

Der synoptische Anblick des Ozeans aus dem Weltraum

Von Prof. Dr. *Robert E. Stevenson**,
Research Oceanographer, US Fish and Wildlife Service, Bureau of Commercial Fisheries,
Galveston, Texas (USA)

Obwohl unser Wissen vom Ozean, besonders in den letzten Jahrzehnten, rapide zugenommen hat, stehen die Ozeanographen noch immer vor dem Problem, das sich bereits gegen Ende des 19. Jahrhunderts stellte, nämlich dem Mangel an synoptischen Daten. Vermessungen bei gleichzeitigem Einsatz mehrerer Schiffe können nur einen kleinen Teil des Ozeans erfassen und dies nur für eine begrenzte Zeitperiode. Sie stellen daher keine wirkliche Lösung des Problems dar. Es wurde vorgeschlagen, ein weltumspannendes Netz von automatischen Hochseebojen zu schaffen. Ein Bojennetz, das den meteorologischen Stationen auf den Landgebieten der Erde vergleichbar wäre, würde einige 30 000 Bojen erfordern. Wegen der erheblichen Kosten sind die Aussichten für die Verwirklichung dieses Projektes nicht sehr groß. Der Einsatz von Weltraumfahrzeugen hingegen gewährt eine völlig neuartige, bisher nicht bekannte Sicht auf Teile der Weltmeere und ermöglicht somit eine echte Synopsis. Einige der Aufnahmen, die bei Einsätzen von Gemini- und Apollo-Raumkapseln gewonnen wurden, zeigen so eindrucksvolle Einzelheiten, daß man nicht umhinkann, über die Zukunft der „Weltraumozeanographie" sehr optimistisch zu sein. Einige dieser Bilder sind auf den folgenden Seiten wiedergegeben.

Die ersten Berechnungen der Wahrscheinlichkeit, daß nützliche ozeanographische Daten aus dem Weltraum gewonnen werden können, waren nicht ermutigend. Photographien, die die Astronauten im Rahmen des Gemini-Programms der NASA gewonnen haben, lieferten indessen Informationen, die uns zu der Ansicht führen, daß überaus nützliche und bis dahin nicht erreichbare Daten durch orbitale Satellitensysteme gewonnen werden können.

Ein die Erde umkreisender Raumflugkörper bietet die Möglichkeit einer umfassenden, ständig sich wiederholenden synoptischen Beobachtung der Weltmeere. Das System zur Gewinnung der notwendigen Daten muß noch entworfen werden. Die bisher dem Ozeanographen zur Verfügung stehende Information stammt aus photographischen Aufnahmen. Registrierungen in anderen Wellenlängenbereichen des elektromagnetischen Spektrums würden das Bild ergänzen und abrunden. Die nachfolgend veröffentlichte Auswahl von Aufnahmen zeigt eindringlich, welche bisher noch nicht ausgeschöpften Möglichkeiten in den Satellitenbildern liegen.

Wolken über der Insel Guadalupe (Bild 1)

Das Meerwasser vor der Küste von Kalifornien und der sich südlich anschließenden Halbinsel Niederkalifornien ist kühl infolge der vorherrschenden Strömung, die im Ostpazifik von Nord nach Süd verläuft. Stratus- und Stratokumuluswolken bilden sich über dem kühlen Wasser und sind fast ständige charakteristische Gebilde der Atmosphäre über dem Meer. Auch die atmosphärische Zirkulation über diesem Teil des Pazifischen Ozeans verläuft gewöhnlich von Nord nach Süd, wenngleich sie auch entsprechend den jahreszeitlichen Änderungen im Hochdrucksystem von Hawaii schwankt und örtlichen Verhältnissen unterliegt, wie sie jeder Küste eigentümlich sind.

Eine tiefe Schicht von Stratokumuluswolken bewegte sich mit 3 bis 5 m/sec an der Insel Guadalupe vorbei, als das Raumschiff Gemini 5 die Gewässer bei Niederkalifornien (Baja California) überquerte.

Die Bergspitzen der Insel, die bis 1500 m emporragen, kommen durch die Wolkenschicht hindurch zum Vorschein und stehen mit ihr in Wechselwirkung. Eine Art Bugwelle, ähnlich wie die von einem Schiff, breitet sich vom Nordende der Insel her aus. Weiter stromabwärts werden südlich der Insel die aus der Aerodynamik bekannten von-Kármán-Wirbel, die sich nach rechts und nach links drehen, als eine Art turbulentes Kielwasser der Insel gebildet. Diese Wolkenbildungen, Wellen und Wirbel wurden bei vier Geminieinsätzen photographiert. Sie müssen daher als eine klimatische Eigentümlichkeit der marinen Atmosphäre von Guadalupe angesehen werden. Ähnliche Wellen und Wirbel erscheinen auch im Wasser bei der Umströmung anderer Inseln. Diese Strömungserscheinungen müssen weiter untersucht werden.

Aufsteigendes Wasser bei Taiwan (Bild 2)

Im westlichen Pazifik verläuft das Hauptströmungssystem von Süd nach Nord an der Insel Taiwan vorbei. In der näheren Umgebung der Insel und insbesondere in der Straße von Formosa werden die Strömungen jedoch durch die Gezeiten kompliziert, die entlang der Südküste von Taiwan nach Süden zu abnehmen.

Am 19. Juli, dem Tag bevor die in *Bild 2* wiedergegebene Aufnahme gemacht wurde, befand sich der tropische Wirbelsturm „Nina" ungefähr 167 km östlich von Taiwan. Der Sturm war nicht gut entwickelt, und Winde der Beaufort-Skala 3 waren die stärksten, die verzeichnet wurden. Am 20. Juli um 12 Uhr Greenwich-Zeit hatte sich der Sturm aufgelöst und Winde der Stärke 2 bliesen von Osten her um Taiwan.

In *Bild 2* ist das helle Blau des Meeres die Folge einer diffusen Sonnenreflexion an einer gleichmäßig rauhen Meeresoberfläche. Winde aus Ost und Nordost haben

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* Geb. 1921; Hauptarbeitsgebiete: Ozeanographie und marine Geologie.
Contribution Nr. 277, Bureau of Commercial Fisheries, Biological Laboratory, Galveston, Texas.

Der Ozean im Gemini-Photo

Hier ein Blick auf Florida (rechts), die Bahama-Inseln (links) und Kuba (oben) aus einer Höhe von etwa 200 km.

Titelbild

Bild 1: Wolkenströmung bei der Insel Guadalupe. Aufgenommen aus einer Höhe von 240 km während des Geminifluges 5 am 21. 8. 1965 durch die Astronauten Lt. Col. L. G. Cooper und Cdr. Charles Conrad, jr. mit 80 mm Brennweite. Norden ist links. National Aeronautics and Space Administration/Manned Spacecraft Center Color No. S65-45697.

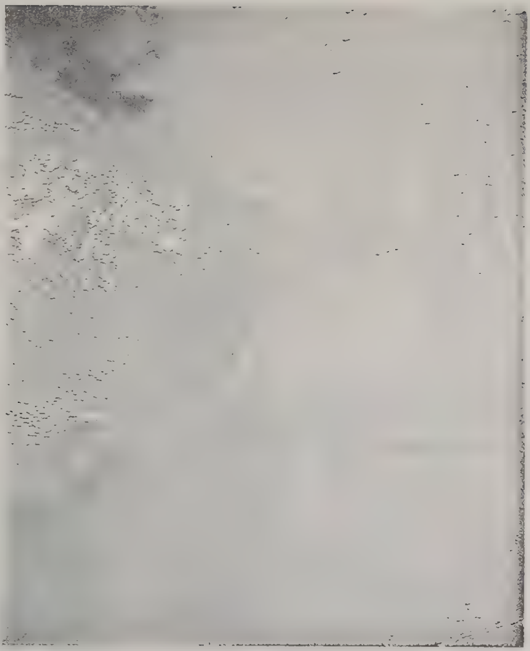


Bild 2: Die Insel Taiwan im Pazifischen Ozean, aufgenommen aus einer Höhe von 190 km beim Geminiflug 10 am 20. 7. 1966 durch die Astronauten Cdr. John W. Young und Maj. Michael Collins, 80 mm Brennweite. Norden ist links. National Aeronautics and Space Administration/Manned Spacecraft Center Color Nr. S66-45868.

Bild 3: Der Atlantik und die Küste von Georgia, aufgenommen aus einer Höhe von 165 km beim Flug des unbemannten Raumschiffes Apollo 502 am 4. 4. 1968, 70 mm Brennweite. Norden ist links. National Aeronautics and Space Administration/Manned Spacecraft Center No. AS6-2-1485.

die Rauhheit der nach Norden strömenden Gewässer erhöht. Das gespiegelte Reflexmuster, das die Meeresoberfläche bietet, gibt somit ein Bild der eigentümlichen Wasserbewegung um das Südende von Taiwan herum.

Der Hauptstrom wird durch die Insel geteilt, so wie ein Schiff das Wasser zerteilt. In dem Maße, wie sich die „Bugwelle" von der Insel her ausbreitet, muß in Küstennähe Meerwasser aus der Tiefe aufsteigen, was in *Bild 2* an der dunkelblauen Farbe kenntlich ist. An der Westküste (in *Bild 2* unten) befindet sich unmittelbar in Küstennähe das Hauptgebiet der Sardinenfischerei der Formosastraße.

Die Küste von Georgia (Bild 3)

Zu Beginn der dritten Umlaufbahn von Apollo 502 überflog das Raumschiff die Küste des Staates Georgia am späten Vormittag. Die Sonne lieferte ein hervorragendes, glitzerndes Reflexmuster an der Meeresoberfläche. Der Wind kam aus Südost (3 m/sec), parallel zu den langen Streifen von Kumuluswolken, die über dem Festland von Georgia lagen und wie lange Girlanden aus Puffmais aussahen.

Die Flußmündungen, die Lagunen, die Wattengebiete und die Georgia vorgelagerten Inseln sind auf dieser Aufnahme deutlich zu sehen. Die rötlichgoldene Farbe rührt her von der Reflexion der Sonne an der Meeresoberfläche und von den Gewässern in den Gezeitenstromrinnen der Marschgebiete und Lagunenkomplexe der Küste.

Es ist deutlich zu sehen, wie sich im Wasser die Sedimente abheben, welche aus den Flußmündungen an der Küste abgelagert wurden. Vor der Küste sieht man lange Schlieren in einer von Nordwest nach Südost laufenden Richtung angeordnet. In Küstennähe hatte das Wasser mit geringem Salzgehalt eine etwas rauhere Oberflächenstruktur als das Wasser weiter draußen. Außerhalb des Gebietes der Sonnenreflexion nördlich entlang der Küste, etwa bei Savannah (links in *Bild 3*), markiert die Trübung des Wassers die äußere Begrenzung der Küstengewässer. Das Abbiegen der glänzenden Muster zeigt den Transport von küstenfernem Wasser in die südlich strömenden Küstengewässer, insbesondere in der Mitte des Bildes.

Entlang der Küste von Georgia gibt es hervorragende Fischgebiete für Menhaden *(brevoortia tyrannus)* und Garnelen, die einen Teil ihres Lebens in den Küstenlagunen und Flußmündungen verbringen. Wenn sie von dort in den offenen Ozean hinauswandern, ist ihr Weg für die Fischer von großer Wichtigkeit. Man kann leicht sehen, wie die lokalen Strömungen in diesem Gebiet sich bis etwa 18 km weit (im Bild etwa 30 mm) über die Küstenlinie der Inselbarriere von Georgia hinaus erstrecken.

Eine Divergenz vor Florida (Titelbild)

Diese sehr schräg aufgenommene Photographie ist nicht nur eindrucksvoll hinsichtlich des erfaßten Gebietes und des allgemeinen Anblicks, den sie bietet, sondern sie hat auch einige sehr nützliche ozeanographische Informationen geliefert. Der Blick geht nach Südwesten. Die Florida-Riffe (Keys), die Marquesas-Inseln und die Dry Tortugas *(Karte 1)* liegen in der Mitte des Sonnenreflexes auf dem Meer. Nach links zu befinden sich die kleine Bahama-Bank, mit der großen Bahama-Insel unter Kumuluswolken, und die kleine und große Abaco-Insel. Eleuthera ist fast völlig unter Wolken verborgen, aber New Providence Island mit der Stadt Nassau sind zwischen zwei Wolkenlinien zu sehen. Die große Bahama-Bank mit den Inseln Andros und Bimini erstreckt sich nach Süden in Richtung auf die Ostprovinz von Kuba. Ost- und Zentralkuba haben eine dichte Wolkendecke, aber das Gebiet um Havanna und die Isla de Pinos ist ziemlich klar. In der Nähe des Horizontes, weit nach Westen zu, befindet sich die Halbinsel Yucatán, die auf unserem *Titelbild* nur noch ganz schwach zu erkennen ist.

Der Wind wehte nach Südwest über die Bahama-Inseln, aber er drehte sich über Kuba und Florida mehr nach West. Auch ohne Daten von Wetterstationen sind die Strömungslinien des Windes deutlich aus den Wolkenlinien abzulesen. Schlierenartige helle Streifen deuten auf geringere Wellentätigkeit und demzufolge glatteres Wasser hin; sie sind auf der dem Wind abgewandten Seite (Lee) von Inseln, Untiefen und Landspitzen zu sehen. Diese Muster sind nur deshalb sichtbar, weil die Reflexe in das Gesichtsfeld fallen. Die Spiegelung differiert entsprechend den Oberflächen unterschiedlicher Struktur. Infolgedessen können helle Flecken (= ruhiges Wasser) ausgemacht werden westlich von Cap Sable in Florida und westlich der Halbinsel von Zapata, Isla de Pinos und Cabo San Antonio.

Ein anderes, hellglänzendes Gebiet liegt vor der Westküste von Florida. Hier ist das Wasser bewegt und verursacht eine diffuse Reflexion des Sonnenlichts. Dazwischen befindet sich dunkleres, blaues (ruhigeres) Wasser. Aus der Tatsache, daß sich dieses ruhige Wasser nicht in Küstennähe befindet und somit nicht als Lee-Effekt entsteht, ergibt sich die Folgerung, daß dieses Wasser sich mit dem Wind bewegt. Folglich ist der dem Lande zugewandte Rand des dunkelblauen Wassers eine Divergenz, an der Wasser aus tieferen Gebieten zur Oberfläche aufsteigt. Es ist kaum ein Zufall, daß sich hier ein wichtiges Fischereigebiet befindet.

Die Nase des Raumfahrzeuges weist auf den küstennahen Teil einer Linie von Kumuluswolken, die beständig die landseitige Grenze des Golfstroms markiert. Nur wenn tropische Störungen oder Zyklonen sich durch den Himmel von Florida bewegen, verschwindet diese Kumulusreihe. Sie kehrt aber bald wieder als ein typischer Zug des dortigen Klimas.

Der Ozeanograph, der Meteorologe und auch der Geologe können aus dieser Aufnahme sehr viel lernen.

Der trübe Golf von Martaban (Bild 4)

Diese über Birma gewonnene Photographie gibt ein vorzügliches Bild des Tieflandes, mit dem das Hauptdelta des Irawady wie ein Lappen etwa 150 km nach Süden in die nördliche Andamanensee hineinragt *(Karte 2)*. Ferner sind das trübe Wasser im Golf von Martaban und die nordwestliche Küstengegend der birmesischen Halbinsel gut ausgeprägt. Da die Aufnahme frühmorgens gemacht wurde, ist das östliche Landgebiet ziemlich dunkel. Das ganze Gebiet ist ungewöhnlich frei von Wolken. Dies ist typisch für den Monat November nach dem Sommermonsun.

Das trübe Wasser im Golf von Martaban entstammt offensichtlich Flüssen, die nach Süden in den Nordteil des Golfes strömen. In dieser Jahreszeit und während einiger Monate nach dem Südwestmonsun ist der Irawady stark mit Sinkstoffen beladen. Man kann gut erkennen, wie trübe Wasser aus dem Mündungsdelta des Irawady in den Golf von Martaban einströmen. Der Südwestmonsun hat West-Ost-Strömungen erzeugt, welche die schwebenden Sedimente in den Golf von Martaban hineintransportieren.

Die allgemeine Zirkulation in der Bucht von Bengalen, wie sie in den Segelanweisungen für dieses Gebiet angegeben ist, verzeichnet eine Wasserströmung nach Westen aus dem Golf von Martaban heraus. Die Windrichtung für November ist auf den Karten der genannten Segelanweisung als ebenfalls westlich angegeben. Die Aufnahme *Bild 4* zeigt, daß offensichtlich das Gegenteil der Fall ist.

Die Sedimentation (hauptsächlich schlickiger Sand und toniger Schlick) beschränkt sich auf das Delta des Irawady und den Golf von Martaban, wie diese Gemini-Aufnahme zeigt. Die Grenze der Sedimentation stimmt ziemlich genau mit der äußeren Begrenzung des trüben Wassers überein.

Die Grenze des trüben Wassers liegt auch recht genau über einem steilen Abfall des Schelfgebietes. 30 km vor der Mündung des Irawady-Deltas findet sich ein deutlicher Abfall des Meeresbodens. Näher an der Küste ist der Meeresboden infolge junger Sedimentierung flach und seicht. Der äußere Deltaschelf hat beträchtlich mehr Relief, wird aber ständig durch Sedimentation verändert.

Im Laufe des Juli 1967 verbrachten Wissenschaftler an Bord des amerikanischen Küsten- und geodätischen Vermessungsschiffes, Oceanographer, zwei Wochen mit dem Studium der Gewässer vor dem Irawady-Delta. Die Analyse der Daten der Fahrt ist noch nicht abgeschlossen; die Gemini-Farbaufnahme wird bei der Auswertung eine große Hilfe darstellen.

Fischgründe und Küstenverlauf (Bild 5)

Der südliche Golf von Kalifornien mit der Stadt La Paz zur Rechten und dem mexikanischen Festland zur Linken wurde von den Gemini-11-Astronauten am 14. 9. 1966 beobachtet. Der Rand der Sonnenreflexion von der Meeresfläche befindet sich im oberen Teil der Aufnahme.

Von Interesse sind hier die hellen Strukturen zwischen der Küste von La Paz und der Insel Cerralvo (La Paz am oberen Ende der Bucht, Cerralvo oben rechts), die gerade Wolkenreihe nördlich davon und die große Konvergenz unter einer langen Reihe von Kumuli, die sich quer über den Golf zu den Lagunen der mexikanischen Festlandküste erstreckt. Das Reflexionsmuster deutet Wasserbewegung durch die Meeresenge hindurch an mit einem turbulenten Wirbel nördlich Cerralvo. Eine Konvergenz-Linie im Wasser und in der darüberliegenden Luft befindet sich nordöstlich der Insel.

Besonders eindrucksvoll ist aber die Konvergenz, die sich in nordost-südwestlicher Richtung auf das mexikanische Festland hin erstreckt. Die Flut strömt nach Norden (in *Bild 5* unten) in den Golf von Kalifornien ein. Zu der Zeit dieser Aufnahme begegneten sich zwei verschiedene Wassermassen in dem Gebiet, das durch die Reihe von Kumuluswolken markiert ist: einerseits die einströmende Flut, andererseits das von der vorangegangenen Ebbe übriggebliebene Wasser. Das Ergebnis ist eine kräftige Konvergenz von Wassermassen unterschiedlicher Temperatur, die durch eine darüberliegende Kumulusreihe markiert ist.

An diesem Tage herrschten östliche Winde, und daher bildete sich die Kumuluslinie auf der warmen Seite der Konvergenz. Allerlei Treibgut und Nahrungsstoffe, die in der Konvergenz konzentriert sind, liefern ein hervorragendes Futter für große Schwertfische u. ä. Die Konvergenzlinie markiert die großen Marlin-Fischgründe von Niederkalifornien.

Wasserströmungen um die Bahama-Bänke (Bild 6)

Ein hervorragendes Beispiel für Wechselwirkungen von Land- und Seeluft liefern Aufnahmen eines Teiles der Bahama-Inseln. In *Bild 6* kann man die Bucht von Florida, die Florida-Riffe und die Florida-Straße unter der offenen Tür des Raumschiffes sehen. Auf der anderen Seite der Florida-Straße befindet sich der nördliche Teil der großen Bahama-Bank, die Insel Bimini, die Inselgruppe der Berrys, der nördliche Teil der Andros-Inseln, die Insel New Providence mit der Stadt Nassau. Unter der Nase der Agena-Rakete befinden sich die große Bahama-Insel, die kleine Bahama-Bank und Wolken, die über den Wassern des Golfstroms liegen.

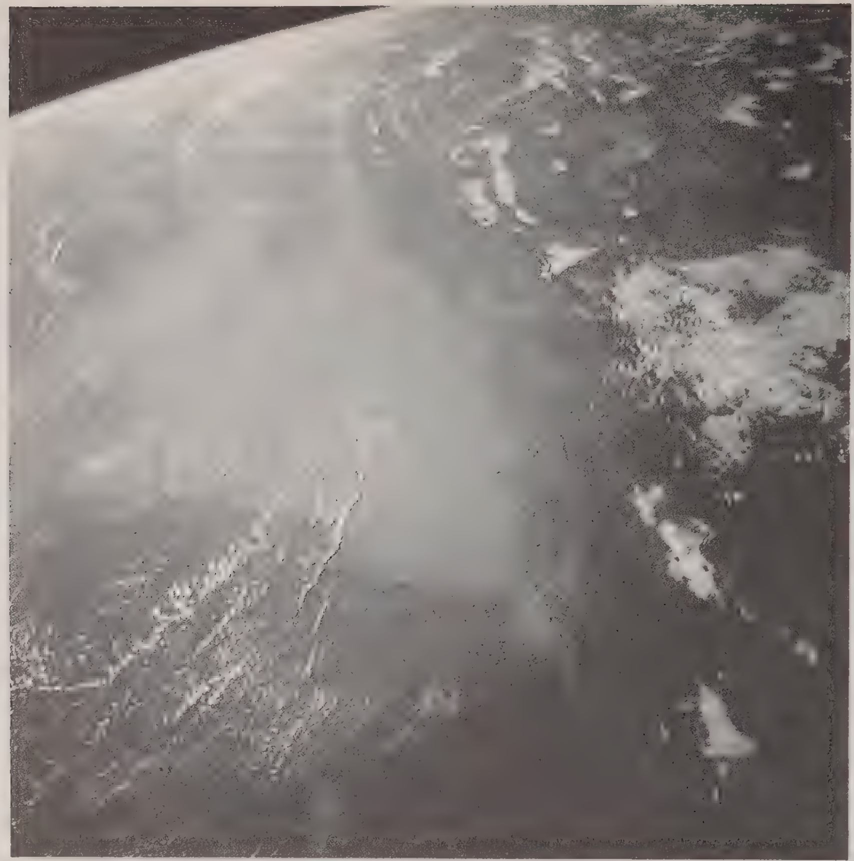
Diese Aufnahme ist besonders interessant wegen der klar umrissenen, flachen, kalkhaltigen Sandbänke der großen und kleinen Bahama-Bank. Unmittelbar südlich der Insel Bimini befindet sich eine Anzahl großer mehr oder weniger U-förmig ausgebildeter Streifen, die das Hinüberströmen von Wasser in das Flachwassergebiet der großen Bahama-Bank hinein kennzeichnen. Ähnliche Überströmungsmarken gibt es rund um die Berry-Inselgruppe und um die Nordspitze der Insel Andros. Offensichtlich fließt in jedem dieser Gebiete auflaufendes Wasser zum Zentrum der großen Bahama-Bank. Unmittelbar unter der Tür des Raumfahrzeugs sieht man eine lange Sandbank, an der auflaufendes Wasser zusammenströmt. Bei Ebbe fließen diese Wassermassen in den Kanal zwischen der großen Bahama-Bank und der großen Bahama-Insel zurück, gelangen in den Golfstrom und damit weiter nach Norden in den Atlantischen Ozean.

Die flutenden Wassermassen, die diese großen, prächtigen Strukturen bilden, sind das Ergebnis starker Sturzseen, die hauptsächlich durch Hurrikan-Winde auf dem Meer gebildet wurden. Es gibt also eine ganze Folge von zusammenwirkenden Ereignissen, die der Gestalt der durch die Gezeiten überströmten Untiefen ihr Siegel aufpressen. Wenn man die 8 bis 60 km langen Sandbänke betrachtet, kann man sich leicht ein Bild machen von der Stärke der atmosphärischen Winde über der See, die die brandenden Wassermassen erzeugen, welche dann über die flachen Bahama-Bänke rollen.

Wolken, Winde und Konvergenzen (Bild 7)

Die Verteilung von suspendierten Sedimenten in Küstengewässern und die veränderliche Trübung des Wassers können dazu dienen, die Bewegungen von Küstengewässern zu bestimmen. Was es bedeutet, 6000 km² Küstenwasserbewegung in einem Augenblick zu übersehen, kann kaum hoch genug eingeschätzt werden.

Entlang der Küste von Surinam (Nordküste von Südamerika) breitete sich am 21. Juli 1966 das von den Flüssen abgegebene, mit Sedimenten beladene Wasser entlang der Küste nach Westen aus. Etwa 15 km weiter von der Küste entfernt zeigt die Trübung des Wassers eine Strömung nach Osten an (diese feinen Strukturen gehen leider im Klischee verloren). Die allgemeine Strömungsrichtung in diesen Teilen des tropischen Atlantik



4 *Bild 4: Die Bucht von Bengalen, Birma und die Flüsse Irawady und Rangoon, aufgenommen aus einer Höhe von 350 km beim Geminiflug 12 am 13. 11. 1966 durch die Astronauten Capt. James A. Lovell, jr. und Lt. Col. Edwin E. Aldrin, jr. mit einem Biogon-Weitwinkel-Objektiv, 38 mm Brennweite. Norden ist oben. National Aeronautics and Space Administration/Manned Spacecraft Center Color No. S66-62979.*

Bild 5: Der Golf von Kalifornien; Norden ist unten. Rechts Niederkalifornien, die Stadt La Paz (am oberen Ende der Bucht), die Inseln Santa Cruz (ganz unten), San Diego, San José, Espiritu Santo und oben schließlich die Insel Cerralvo, aufgenommen aus einer Höhe von 300 km beim Geminiflug 11 am 14. 9. 1966 durch die Astronauten Cdr. Charles Conrad, jr. und Cdr. Richard F. Gordon, jr., 80 mm Brennweite. National Aeronautics and Space Administration/Manned Spacecraft Center Color No. S66-54810.

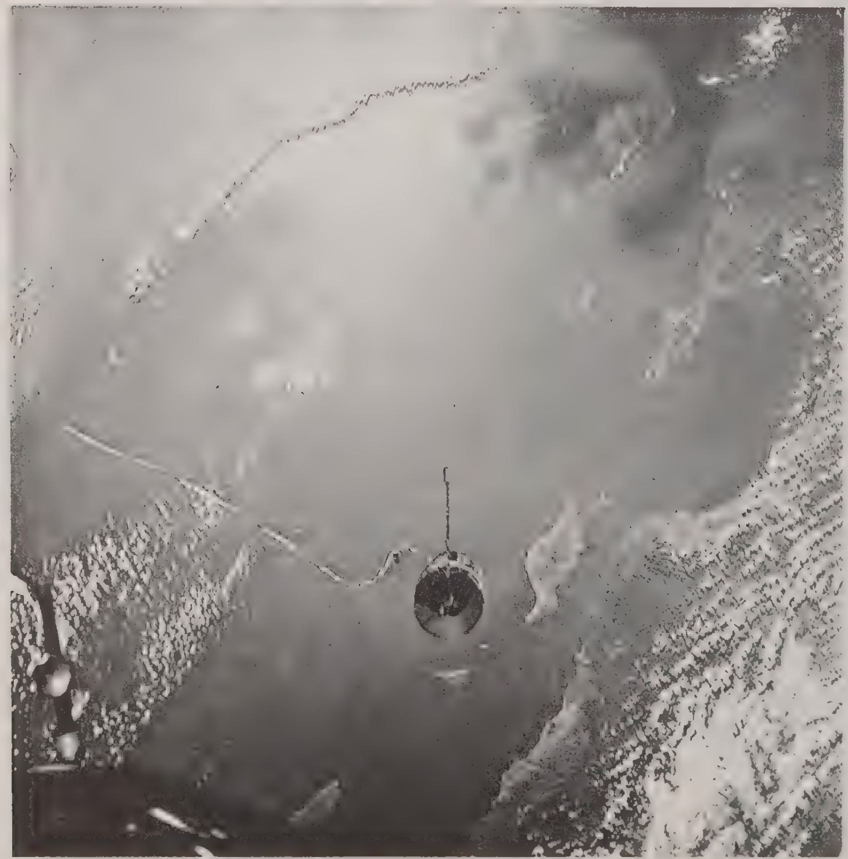
▶

Bild 6: Die Bahama-Insel, die Bucht von Florida, die Florida-Riffe und die Meerenge von Florida, aufgenommen aus einer Höhe von 330 km beim Geminiflug 12 vom 12. 11. 1966 durch die Astronauten Capt. James A. Lovell, jr. und Lt. Col. Edwin E. Aldrin, jr. mit einem Biogon-Weitwinkel-Objektiv, 38 mm Brennweite. Norden ist unten. National Aeronautics and Space Administration/Manned Spacecraft Center Color No. S66-62908.

Bild 7: Die Küste von Surinam an der Nordküste Südamerikas, aufgenommen aus einer Höhe von 250 km beim Geminiflug 10 vom 21. 7. 1966 durch die Astronauten Cdr. John W. Young und Maj. Michael Collins, 80 mm Brennweite. Norden ist oben. National Aeronautics and Space Administration/Manned Spacecraft Center Color No. S66-46056.

Bild 8: Indien, Ceylon und ein Teil des Indischen Ozeans, aufgenommen aus einer Höhe von 680 km beim Geminiflug 11 am 14. 9. 1966 durch die Astronauten Cdr. Charles Conrad, jr. und Cdr. Richard F. Gordon, jr. mit einem Biogon-Weitwinkel-Objektiv, 38 mm Brennweite. National Aeronautics and Space Administration/Manned Spacecraft Center Color No. S66-54677.

Bild 9: Insel Guadalupe im Pazifik, Niederkalifornien und ein Teil des Festlandes von Mexiko, aufgenommen aus einer Höhe von 340 km beim Geminiflug 12 am 13. 11. 1966 durch die Astronauten Capt. James A. Lovell, jr. und Lt. Col. Edwin E. Aldrin, jr. mit einem Biogon-Weitwinkel-Objektiv, 38 mm Brennweite. Norden ist links. National Aeronautical and Space Administration/Manned Spacecraft Center Color No. S66-63492.



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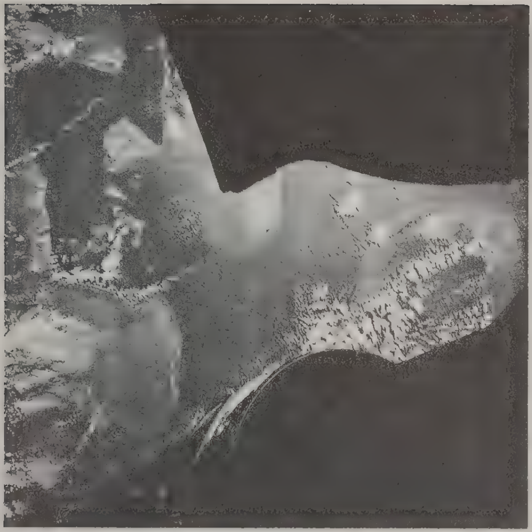

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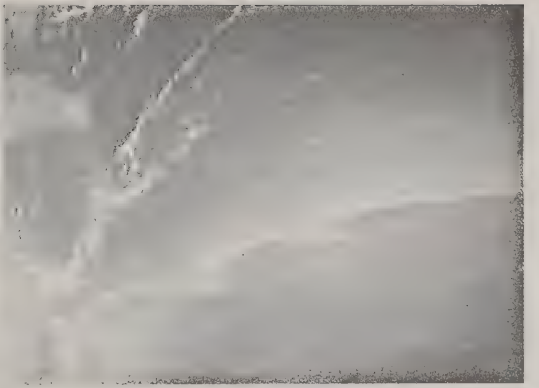

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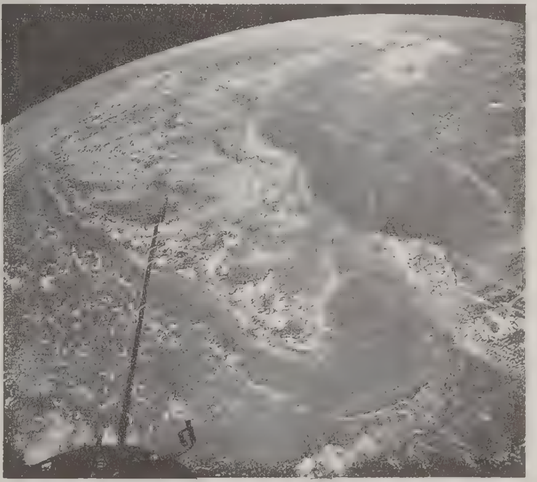

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ist nach Westen gerichtet mit Geschwindigkeiten von 0,5 bis 1,5 m/sec. Das von den trüben Wassermassen erzeugte Muster stellt daher Stromscheren parallel zur Küste dar.

Die Umstände, unter denen diese Strömungen und Scherungszonen entwickelt werden, sind nicht bekannt, und eine beträchtliche Arbeit detaillierter ozeanographischer Forschung muß noch geleistet werden, um die aus dem Raumfahrzeug gewonnenen Daten richtig zu deuten. Man vermutet als Ursache der Stromscheren vor den Küsten von Surinam die Gezeiten. Hier geht die Flut nach Osten und die Ebbe nach Westen.

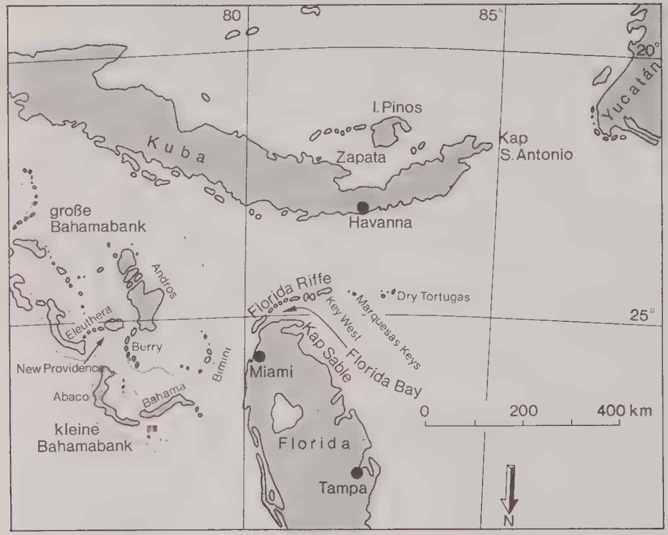
Die sich nach Nordost erstreckenden Kumulusreihen erzeugen eine Konvergenz der unteren Atmosphäre, die man auch als die maritime Reibungsschicht betrachten kann. Es handelt sich nicht um bedeutende Konvergenzen, wie etwa bei einem Frontensystem, und die dabei entstehenden Winde und Drücke würden auf der üblichen synoptischen Wetterkarte nicht erscheinen.

Unter gewissen Umständen setzen die in die atmosphärische Konvergenz einströmenden Winde das oberflächennahe Wasser in Bewegung und bilden so eine Konvergenz im Meer. Diese Verhältnisse herrschten offensichtlich vor Surinam am 21. Juli, wo die Wolkenreihen deutlich mit Grenzlinien trüben Wassers verbunden sind.

Meeresbrise über dem Indischen Ozean (Bild 8)

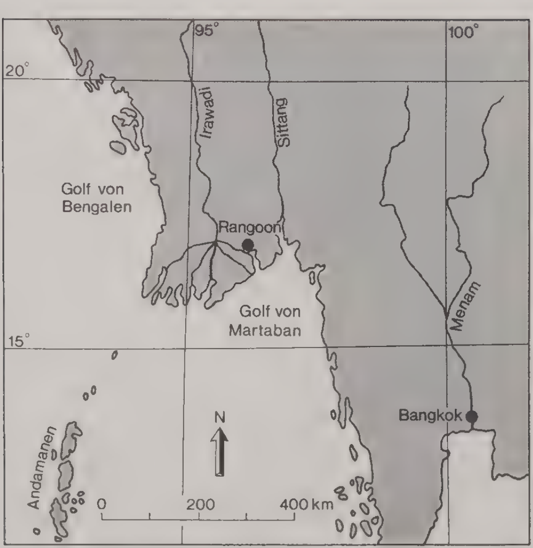
Der wolkenlose Himmel über der ganzen Küste von Indien ist wahrscheinlich das Ergebnis absinkender Luft, wie sie während der tagsüber wehenden Meeresbrise zu erwarten ist. Die Wetterkarte von 12 Uhr Greenwich-Zeit — 5 Stunden, nachdem *Bild 8* aufgenommen wurde — zeigt, daß die Winde an allen Küsten landeinwärts wehten. Über Zentralindien war die Luft ruhig, und es herrschte ein leichtes Tiefdrucksystem über dem nördlichen Teil des Subkontinents. Die Lufttemperatur betrug ungefähr 27 °C, und im Inland waren die Temperaturen 3 bis 5 °C höher. Die Verhältnisse waren typisch für einen Tag mit Meeresbrise.

Die Möglichkeit, ein solches System im ganzen zu „se-



Karte 1: Südspitze von Florida, Bahama-Inseln und Kuba zum besseren Verständnis des Titelbildes und des Bildes 4. Aus Vergleichsgründen steht die Karte auf dem Kopf.

Karte 2: Birma und Thailand; zu Bild 4.



hen" ist ungeheuer wichtig. Man kann nicht nur zum ersten Male messen, wie weit die Meeresbrise auf der Seeseite reicht, sondern für eine ganze Küste lassen sich die Winddrift an der Meeresoberfläche, Gebiete möglicher Aufquellvorgänge und Konvergenzen, synoptisch auftragen. Gäbe es eine solche Übersichtsschau täglich, wäre ihr Wert für Fischerei, Schiffahrt und Meteorologie unschätzbar.

Seeseitig der Zone der Meeresbrise zeigen polygonale Bénardzellen von Kumuluswolken eine gleichmäßige Verteilung von Wassertemperatur und das Fehlen von Oberflächenwinden an.

Bénardzellen über Niederkalifornien (Bild 9)

Die Wolken westlich und nordwestlich der Insel Guadalupe (in Richtung auf das Raumfahrzeug) hatten an dem Tag dieser Aufnahme konvektive, polygonale Bénardzellen gebildet. Es handelt sich dabei um ein Wolkenmuster, das nur bei reiner Konvektion ohne horizontale Luftbewegungen entsteht und das nach dem Franzosen *Bénard* benannt ist. Entweder herrschen Aufwinde im Zentrum und Abwinde an den Rändern oder umgekehrt.

Eine Anzahl von Gebieten offener Zellen war zwischen den gewöhnlich geschlossenen Zellen der Stratokumulusschicht verteilt. Die meisten Zellen westlich der Insel waren regelmäßig geformt, manche waren typisch hexagonal.

Die erforderlichen Voraussetzungen für die ideale Entwicklung von Bénardzellen über dem Meer sind die gleichen wie sie *Bénard* (1900) und *Avsec* (1939) festgestellt haben und z. T. von *Schneck* und *Veronis* (1967) auf Grund theoretischer Überlegungen angegeben wurden.

Die untere Begrenzungsfläche (das Meer) muß gleichmäßig erwärmt sein mit einem nur schwachen Temperaturgradient. Die darüberliegende maritime Atmosphäre darf keine wesentliche horizontale Bewegung (Wind) aufweisen; sie sollte hinreichend Feuchtigkeit enthalten, um Kondensation zu ermöglichen, und sie sollte kühler sein als das Meer, so daß es zu entsprechender Konvektion kommt. Jede Abweichung von diesen Bedingungen bewirkt entweder, daß die Zellenstruktur vom Ideal abweicht oder daß es überhaupt keine sichtbaren Zellen gibt.

Nördlich von Guadalupe waren die Zellen deformiert und zeigten nach Süden gerichtete Verlängerungen. Zwischen der Insel und der Westküste von Niederkalifornien bezeichnet eine starke Verlängerung der Bénardzellen eine gut ausgeprägte atmosphärische Scherung, die Guadalupe nördlich und südlich passiert.

Das Nebeneinander von offenen und geschlossenen Bénardzellen liefert eine Grundlage für interessante Überlegungen, besonders hinsichtlich der fast ständigen Temperaturinversion über diesen kühlen Wassermassen. Gewöhnlich ist über tropischen Gewässern die Konvektion vertikal ungehindert, im Gegensatz zu dem völligen Abschluß bei den Experimenten, welche *Bénard* und *Avsec* durchgeführt haben, wobei eine durchsichtige Abdeckung über einer Wolkenkammer angebracht war. Normalerweise würde über dem Ozean kein solcher „Deckel" vorkommen. Folglich würde das Gleichgewicht oder vollentwickelte Zellen, wie sie *Avsec* beschrieben hatte, nicht zu erwarten sein, d. h. die atmosphärischen Zellen würden im Zentrum offen sein.

Das Literaturverzeichnis kann bei der Redaktion angefordert werden.

Use of a Small Submarine for Biological and Oceanographic Research

By

Donald W. Strasburg, Everet C. Jones, and Robert T. B. Iversen

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Bureau of Commercial Fisheries Biological Laboratory Honolulu, Hawaii

The Bureau of Commercial Fisheries Biological Laboratory in Honolulu is concerned with exploring and developing the Pacific Ocean's high seas fishery resources, especially skipjack tuna. Various factors suggest that a specially-constructed research submarine would be a highly useful tool in studying these resources. Plans for a large research submarine are being formulated, and in the meantime a programme of testing and operating small submersibles has also commenced.

The first submarine tested was the two-man vessel "Asherah", which was chartered in 1965. "Asherah" operated in conjunction with a mother ship for one month in the coastal waters of Oahu. Operational problems were minor, and the submarine completed 50 dives during the charter period. Dives were made by day and night, with many to the vehicle's full operational depth of 192 m. Missions included investigations of the plankton community and of tuna and tuna forage organisms, surveys of the sea floor and its resources, measurements of currents and other features while drifting, bioacoustic research, and various incidental studies.

Although the charter was primarily undertaken to obtain submarine operating experience, there were several unexpected research dividends. Of greatest interest were observations on the vertical distribution of tuna and their forage, and on the surprisingly extensive resources on the bottom. These included spiny lobsters, pen shells, red coral, and heart urchins. The operation was highly successful and will be repeated with submarines having a variety of performance capabilities.

Introduction

The Bureau of Commercial Fisheries Biological Laboratory in Honolulu is charged with exploring and developing the high seas fishery resources of the Pacific Ocean. Among the resources receiving attention are several species of pelagic fish: tunas, billfishes, sharks, and others. Emphasis has been placed on skipjack tuna, *Katsuwonus pelamis* (Linnaeus), a widespread and abundant small tuna which is not fully exploited. Recent advances in technique for studying skipjack tuna include underwater viewing facilities on ships (STRASBURG and YUEN, 1960a, 1960b), and shoreside ponds for studying fish under controlled conditions (NAKAMURA, 1962, 1964).

These facilities provide valuable data on tuna behaviour, physiology, and ecology. On the high seas, however, information can be obtained only when fish are near the surface, and a diving school is lost to view almost immediately (STRASBURG, 1961). Other restrictive factors are storms, which exclude ships

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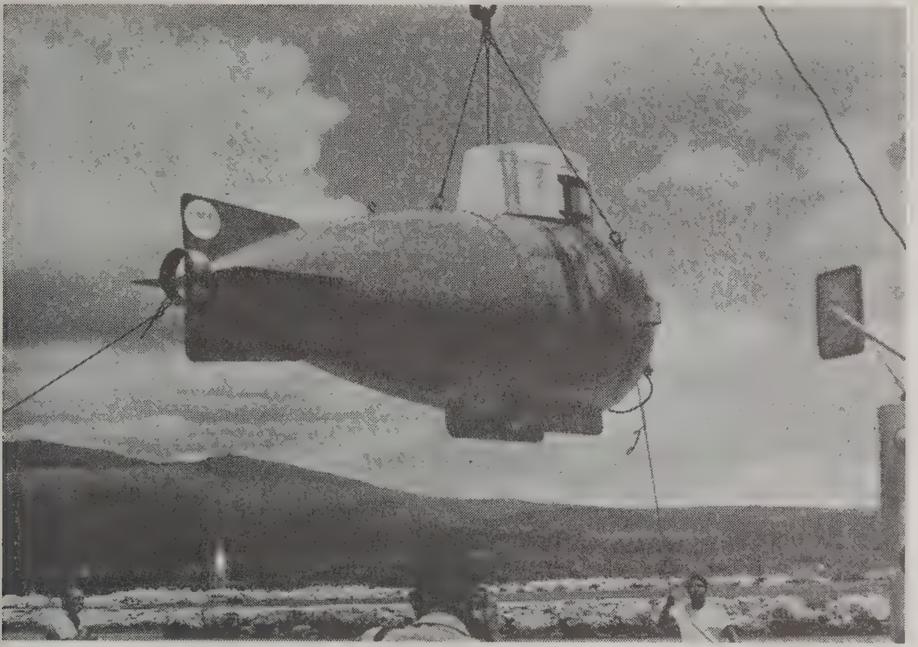

Figure 1a. "Asherah" being unloaded at Campbell Industrial Park.

from many survey areas in winter; ship motion, which prohibits the use of microscopes and other instruments; and ship noise, which interferes with attempts to study bioacoustics.

These and other reasons have caused the Bureau to initiate a programme of fishery research and development in which the biologist and oceanographer are placed directly into the resource environment. Their vehicle is to be a modern submarine specifically designed for research and exploratory missions. A feasibility/conceptual design study for such a submarine has recently been completed (STRASBURG, 1965), using as vessel parameters the known and inferred behaviour of skipjack. The submarine conceived will have a submerged speed of 36 km/hr*, an operational depth of 300 m, a dive endurance of six weeks, and a cruising range of 45,000 km. It will also be highly maneuverable, quiet, and capable of carrying seven scientists in addition to the crew. The feasibility study found that all of the planned performance criteria could be met and some exceeded. The proposed vehicle will be nuclear-powered, highly sophisticated in design and operation, and will require about five years to build.

The Bureau's submarine development programme has several facets. Some aspects of the nuclear submarine concept require engineering studies before design and construction can begin. A set of instruments must be developed and integrated to give the submarine its full scientific potential. Some interim experience in operating submarines is needed to verify the initial performance

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*Although all measurements are here expressed in metric units, they were originally made in English units.

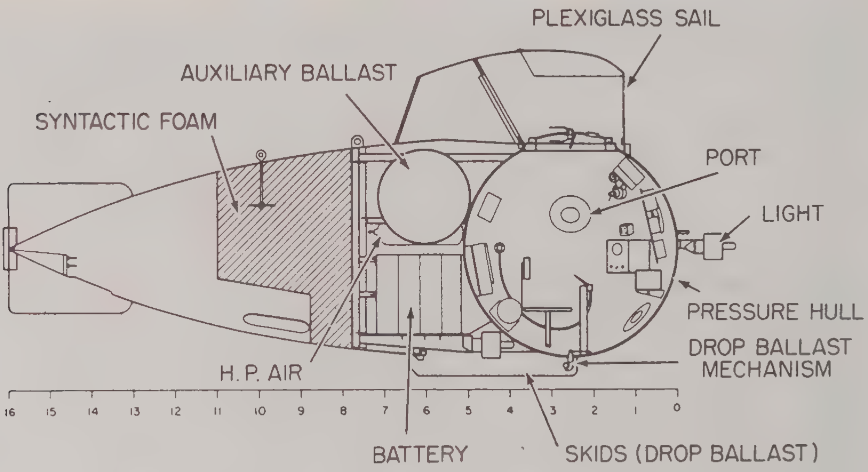

Figure 1 b. "Asherah" in longitudinal section. The scale is in feet.

criteria and to learn in practical terms how a submarine should undertake its missions. A modest programme of testing and operating small submersibles has been started to satisfy the latter requirement. Our first venture into submarine operations is the subject of this report.

Operations with "Asherah"

For our first submarine experience it was desirable that the vehicle be small and simple to operate. The planned missions included surveys of the midwater and bottom fauna, patrols around submerged lights, various oceanographic measurements, bioacoustic studies, and evaluation of fishing and sampling gear. For such tasks an operating depth less than 300 m was considered adequate, as were a speed of 3·5–7 km/hr and a dive endurance of a few hours. A twin-screw vessel was desirable from the standpoint of maneuverability.

The submarine "Asherah" was selected from the vehicles available for charter. "Asherah" was built for the University of Pennsylvania Museum by Electric Boat Division, General Dynamics Corporation, Groton, Connecticut, USA, and was chartered from Electric Boat Division. Several views of "Asherah" are shown in Figure 1; details of her construction and performance are as follows:

Length, over-all	4·9 m
Beam, over-all	2·3 m
Weight in air	5 metric tons
Pressure-hull diameter	1·5 m
Pressure-hull thickness	1·6 cm
No. of occupants	Two: one operator, one observer
Maximum operating depth	183 m
Speed	4·6 km/hr
Propulsion	Two side-mounted, 2-HP, electric motors
Power source	Twelve 24-volt, lead-acid batteries

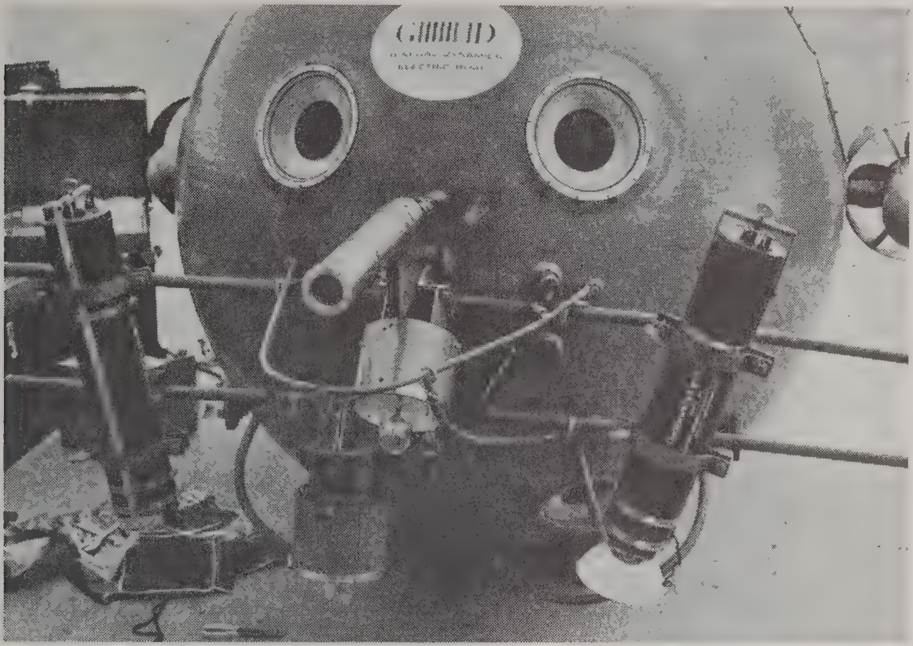

Figure 1c. "Asherah's" external equipment. Left to right: 35-mm film camera, television camera, two floodlights, and stroboscopic flash.

Propulsive endurance	10 hrs (at economical rate)
Life support	48 man-hours
View ports	Six 12·7 cm diameter, 5·1 cm thick, plexiglass
Communication	Underwater telephone, radiotelephone
Navigation	Gyrocompass, fathometer, speed sensor, acoustic pinger
External equipment	Two 400 to 1,200-watt floodlights, film camera, stroboscopic flash, television camera.

"Asherah" was shipped from Groton to Honolulu and trucked thence to the Campbell Industrial Park basin, near Barbers Point, Oahu (Figure 2). After installation of equipment (Figure 1c), the submarine was placed in the basin by a crane, and was then towed offshore to the anchored BCF research vessel "Townsend Cromwell", a 48 m ship which provided support facilities. When not diving, "Asherah" was moored to the "Cromwell's" boom (Figure 3). Preparatory to diving, a boat towed the submarine to the diving site (Figure 4), and also ferried personnel and equipment from the "Cromwell" to the submarine. Another boat, equipped with an acoustic tracking device, an underwater telephone, and a radiotelephone, monitored the submarine's submerged position and relayed messages between the submarine and the "Townsend Cromwell". A continuous record was kept of the submarine's position during dives, both for scientific and safety reasons. Three or four dives were made each day, after which the submarine was towed back to the mother ship, where

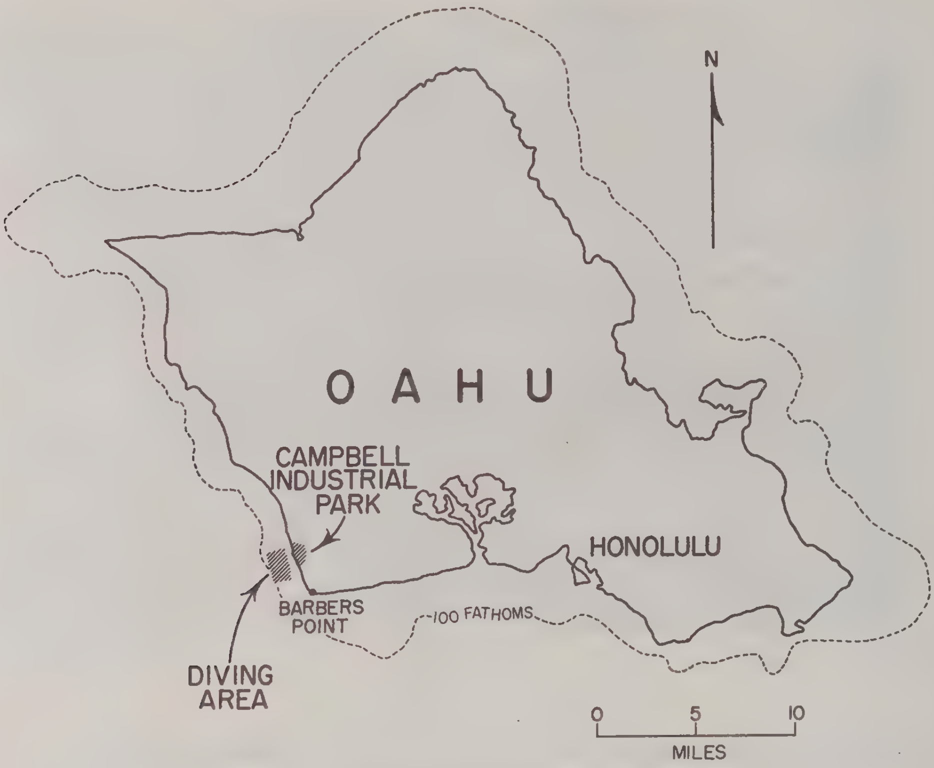

Figure 2. Oahu, showing location of diving area.

her air tanks and batteries were charged for the next day's dives. The air tanks were charged each day, while the batteries were charged every second day.

The Campbell Industrial Park area was selected because of its lee location during trade wind weather, a highly desirable feature for a craft with low freeboard. During our operational period of 18. September through 17. October 1965, however, this area was subject to recurrent variable winds. On a typical day a flat calm sea existed at dawn, and wave height was less than 0·3 m during the morning. The wave height was 0·3–0·9 m by noon, and 0·9–1·5 m thereafter. Access into "Asherah" was difficult with 1 m waves, and hazardous if they were higher. Usually, therefore, the diving day commenced early and ended about noon. Whenever night observations were required, they were made on dives conducted before dawn.

A few operational problems should be mentioned. The submarine's 4·6 km/hr speed was frequently opposed by currents of 0·9–1·8 km/hr, which reduced the vessel's utility. These currents eliminated or hampered several missions in which trawls, longlines, and plankton nets were to be evaluated. Attempts to measure light attenuation by photographing plaques of known reflectance mounted on "Asherah's" bow failed because the distance between camera and plaques was too short for measurable attenuation; passing clouds also had variable effects on the light. Observations were desired on the trajectories of expendable bathythermographs dropped from the surface near the submerged

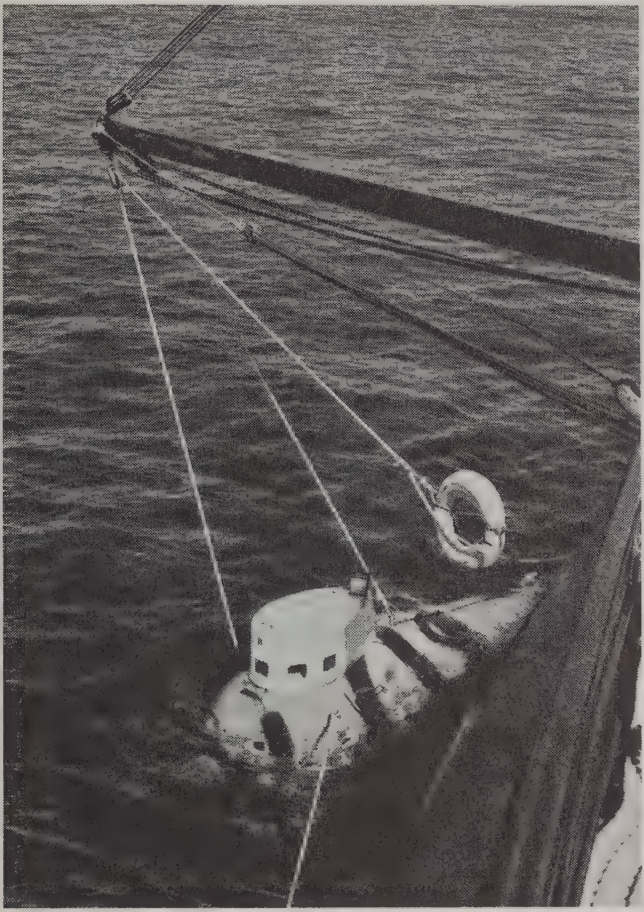

Figure 3. "Asherah" moored to the boom of the R. V. "Townsend Cromwell".

"Asherah". These bomb-shaped instruments travelled too fast for much to be learned. The submarine's high internal humidity necessitated constant wiping of ports and lenses, and prohibited reloading of cameras and tape recorders during dives. The observer had room for only two pieces of equipment, such as a movie camera and a tape recorder, or a movie camera and a still camera. The high ambient temperature prevented adequate cooling of the submarine's floodlights if operated at their 1,200 watt rating. The lights were consequently used only in their 400 watt mode, which greatly reduced the illumination. A burned-out motor and a storm together caused the loss of one of the four weeks of scheduled diving time.

Research Missions and Accomplishments

"Asherah" undertook 50 dives during the month's charter. Dives were made day and night, and many were at full operational depth. Thirty dives carried Bureau staff members whose research was amenable to study by submarine.

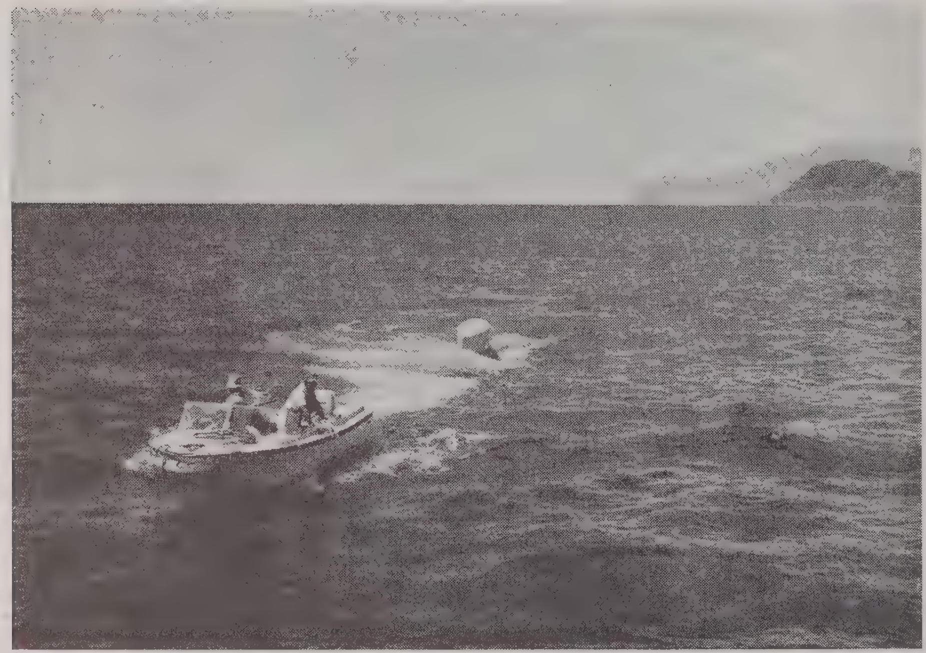

Figure 4. "Asherah" under tow to the diving site.

On the remaining dives the possible research applications of a submarine were demonstrated to others. Multiple missions were prescribed for most dives to make the best use of our limited time. The research undertaken and the general nature of the results were as follows:

Describe the plankton community in relation to various physical features, and describe its diurnal migrations

Plankton was studied during portions of eight dives. Observations were by day and night, between the surface and maximum depth (192 m), and with and without lights. Lights did not attract plankters at great depths, and few plankters were seen around surface night lights. Plankton was generally abundant between 60 and 180 m by day, and was richer at greater depths. Swimming plankters were seen only at night, when the plankton tended to be layered, with concentrations at the surface. Small particles of white material, possibly the "marine snow" of other observers, were encountered in great quantities slowly settling to the bottom. Particle diameter was estimated at about 0·2 mm on the average, but sometimes it was as great as 1 to 2 mm. Counts and spacing-estimates of plankton, made by eye, indicated an average density of about 1,000 mg of plankton per cubic metre of water. This amount is about 50 times as much as is normally caught in net hauls in the open ocean around Oahu (REID, 1962). The discrepancy between the values for observed and captured plankton indicates the extent of escapement or the loss of fragile forms through the net's meshes.

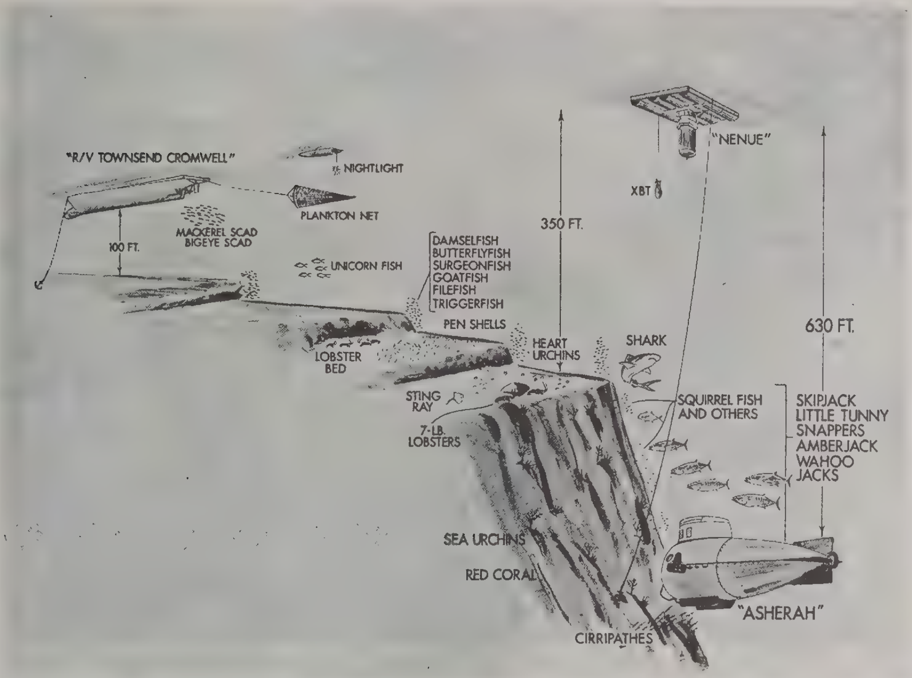
"R/V TOWNSEND CROMWELL"
NIGHTLIGHT
PLANKTON NET
MACKEREL SCAD
BIGEYE SCAD
100 FT.
UNICORN FISH
DAMSELFISH
BUTTERFLYFISH
SURGEONFISH
GOATFISH
FILEFISH
TRIGGERFISH
PEN SHELLS
LOBSTER BED
350 FT.
HEART URCHINS
SHARK
"NENUE"
XBT
630 FT.
STING RAY
7-LB. LOBSTERS
SQUIRREL FISH AND OTHERS
SKIPJACK
LITTLE TUNNY
SNAPPERS
AMBERJACK
WAHOO
JACKS
SEA URCHINS
RED CORAL
"ASHERAH"
CIRRIPATHES

Figure 5. Diagram of diving area and "Asherah" activities. "Nenue" is a manned raft from which observations were made on the trajectories of expendable bathythermographs (XBT's).

Ascertain the availability of tuna, tuna forage, and those species which are present but not eaten by tuna

Skipjack tuna and little tunny, *Euthynnus affinis* (Cantor), were encountered on six dives at surprisingly great depths, 98 to 152 m. The temperature at 152 m was 17·8 °C. Usually these tuna were in groups of 3 to 6 fish, but once they formed a school of 250 fish whose vertical dimension was 30 m and another time 3 tuna were associated with 30 jacks (Carangidae). The school of 250 tuna seemed unafraid of the submarine, and simply opened its ranks to permit the submarine to pass through vertically.

Tuna forage organisms seen (on 13 dives) consisted of four species of small fish, only one of which was identified. These fish occurred between 107 and 192 m. Vast schools swam slowly along the face of a steep cliff. Tuna, amberjack (*Seriola* sp.), and other fish preyed upon them. Three specimens of juvenile *Holocentrus lacteoguttatus* Cuvier were accidentally trapped in the free-flooding sail of "Asherah". One reached the surface alive and lived in an aquarium for two weeks. In the depths, these fish bore the typical pelagic coloration of deep blue and silver. After a few hours of confinement, however, the aquarium specimen developed the red and white stripes by which it is well known on all shallow Hawaiian reefs. Although commonly found in tuna and marlin stomachs, the fish had not been suspected to have a deep-water nursery ground. The three unidentified species of forage fishes were respectively guppy-like, serranid-like, and eleotrid-like. Their length was about 25 to 100 mm.

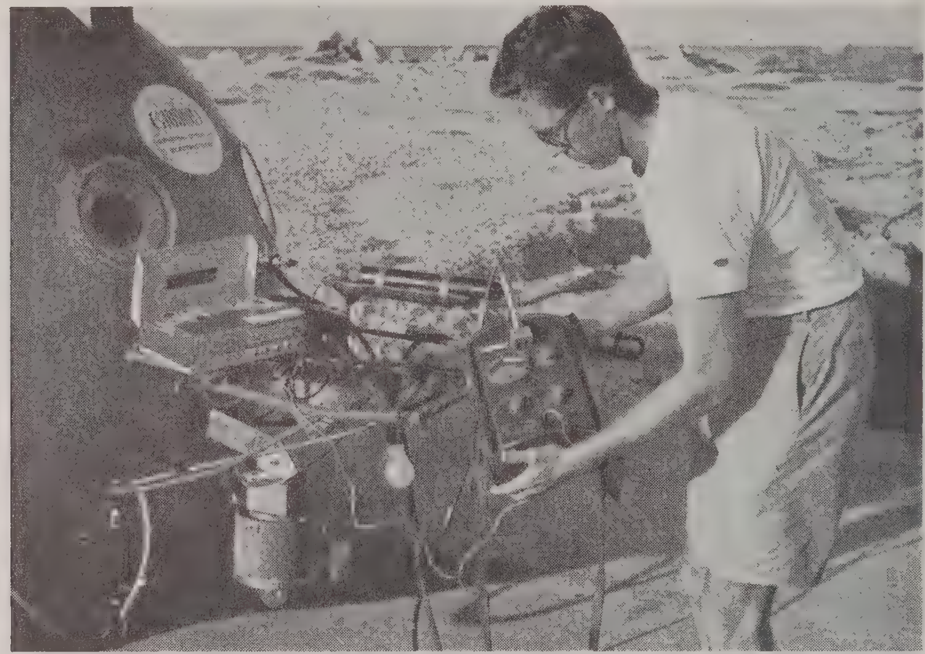

Figure 6. Acoustic equipment on "Asherah". The black cylindrical hydrophone is connected to an amplifier (being held) and to a small tape recorder (in front of the port). The amplifier and tape recorder were carried inside the submarine during dives.

Many estimates of forage school size were made; they ranged from a few hundred fish to more than 10,000. One estimate was expressed in practical fisherman's terms of "300 buckets of bait", or an equivalent of 950 kg of small fish. The schools of forage fish were numerous and constituted a resource of millions of fish.

Two forage species exhibited peculiar behaviour. Before dawn, 150 mm paralepidid fish hovered 10–20 cm above the sandy bottom at 40 to 100 m. Similar paralepidids commonly occur around night lights, and have hitherto been regarded as pelagic rather than demersal. On the dive in which the paralepidids were seen, a mixed school of 200 bigeye scad, *Trachurops crumenophthalmus* (Bloch), and mackerel scad, *Decapterus pinnulatus* (Eydoux and Souleyet), followed the submarine down from the surface. The submarine's lights were on. When "Asherah" reached 110 m, the *Decapterus* inverted, and began swimming in circles about 20 cm in diameter. The *Trachurops* continued to swim normally. On the submarine's ascent, the *Decapterus* continued their inverted swimming, but at 100 m the circles had widened to a diameter of 30 to 60 cm. At 88 m normal swimming was resumed. The fish stayed with the submarine until it reached a depth of 30 m.

Survey of the bottom for fishery resources

Bottom survey was the major purpose of 17 dives, and incidental bottom observations were made on 11 others. The nature of the bottom and its fauna is shown in Figure 5. The surveys covered a depth range of 24 to 192 m. In the shallow (24 to 107 m) inshore surveys the bottom was a sloping sandy plain, interrupted by rocky ledges 3 to 18 m high. The sandy stretches between the ledges were nearly featureless, and were largely devoid of visible fauna. However, wherever there was coral growth or an accumulation of rocky rubble there were aggregations of fish, mostly butterflyfish, damselfish, triggerfish, and surgeonfish. Goatfish, flounders, bonefish, and wrasses foraged over the sand, and in midwater there dwelled large schools of mackerel scad, bigeye scad, jacks, and unicornfish, *Naso hexacanthus* (Bleeker). Fish were concentrated above and in front of ledges, with a cloud of colourful species usually being present. Most fish aggregations were near the cleaning stations of the wrasse, *Labroides phthirophagus* Randall (see RANDALL, 1958).

The invertebrates occurring near rocky patches and ledges between 24 and 107 m were: the starfishes *Culcita* and *Linckia*; *Chondreocidaris* sea urchins; beds of a hydrozoan or anthozoan which resembled *Pennaria* but with larger and heavier individuals; and spiny lobsters, *Panulirus*. The spiny lobsters were up to 60 cm long and an estimated 3·2 kg in weight, as compared with the 0·5 to 0·9 kg of an average reef-caught lobster. In addition, the deep-water spiny lobster occurred on the open bottom whereas the reef lobster is usually taken in caves or beneath ledges. Lobsters were sufficiently numerous to warrant calling their grounds beds; as many as 60 or 70 were sometimes visible. The sandy plains were studded with sponges and the protruding tubes of annelid worms, and tiny (25 mm diameter) brittlestars were abundant. An occasional cone shell occurred on the sand near rocks. Between 60 and 107 m as much as two-thirds of the sea floor was covered by beds of a pen shell, *Atrina*. These black shells were closely packed together, about 540 per m^2, and were often arranged in radially symmetrical patterns. A bed of spatangid heart urchins consisting of thousands of individuals spaced about 30 cm apart occurred at 107 m. Each urchin had a test length of 100 to 150 mm. Although uncommon, the stony coral *Porites* lived down to 107 m. The cleaning shrimp *Stenopus hispidus* (Olivier) was seen at 55 m.

Between 107 and 116 m the sloping plain gave way to a steep cliff, which plunged at 60° to 80° from the horizontal. Much of this cliff was smooth limestone, and was devoid of macroscopic demersal fauna. Wherever the cliff was textured there were silt deposits inhabited by gobies, long-legged shrimp, and lobster-like crustaceans. Ledges, caverns, and other irregularities offering shelter were crowded with squirrelfish, moray eels, butterflyfish, and other fishes. The coils of an antipatharian coelenterate, probably a species of *Cirripathes*, were also common on this cliff. These coils were formed of a black, brown, or copper-colored substance, about 3 mm thick. They spanned about 75 mm, and their length was 150 to 300 mm. Various starfish, sponges, and sea urchins occurred on the cliff down to 192 m. Beds of red coral, *Stylaster* and *Corallium*, existed between 137 and 183 m. The tuna and forage fishes occurring along the cliff are discussed above; in addition, the cliff was patrolled by snappers, amberjack, wahoo, and various jacks. These fish were either solitary or occurred in twos and threes.

Make observations while drifting

In one dive, heavy chain links were put aboard "Asherah" to make her negatively buoyant when the ballast tank was flooded. Prior to diving, a spherical plastic float 127 cm in circumference was attached to the submarine by a 15 m line. For the test, "Asherah" descended to 15 m where she hung suspended, and drifted there for 30 minutes. Radar bearings and ranges were taken on the float at 3 minute intervals by the "Cromwell". The resulting plot indicated a current of 1·06 km per hr at a depth of 15 m. During the test, observations were made on plankton, mackerel scad, and unicornfish which were similarly drifting. Rotation of the submarine about her tether once every 2·5 minutes provided views in all horizontal directions and permitted counts of the biota. It was noted that unicornfish often drifted in odd positions, such as head-down.

Only one such drift trial was attempted, for our sole object was to establish the feasibility of the technique.

Undertake acoustic surveys of the midwater and bottom fauna

Four dives were made to determine the suitability of a small submarine for bioacoustic research. An omnidirectional hydrophone was mounted on struts attached to "Asherah's" bow (Figure 6). The hydrophone's output was coupled to an amplifier and tape recorder inside the submarine. Acoustic monitoring began during the descent and continued as the bottom and slopes were surveyed. When we encountered a sound-producing animal, "Asherah" settled to the bottom with the hydrophone as close as possible to the sound source. This distance was usually 3 m or less. Skillful piloting often placed the hydrophone within small caves containing sound producers. All rotating machinery except the gyroscope was turned off while sounds were recorded. Conversation was whispered to reduce voice radiation by the hull and resultant pickup by the hydrophone.

Sounds were recorded at the locations of the following known or suspected sound-producing fish: three squirrelfish, *Myripristis chryseres* Jordan and Evermann, *Holocentrus lacteoguttatus* Cuvier, and *Holocentrus* sp. (possibly *ensifer* Jordan and Evermann); and one triggerfish, *Balistes bursa* Bloch and Schneider. Often several possible sound-producers occurred as an aggregation, consequently, sounds could not be precisely identified as to source. The recording sites lay between 52 and 107 m deep.

Figure 7 is a spectrogram of a typical fixed-interval staccato sound recording. Eight individual sound pulses, approximately 100 milliseconds in length, form the entire sound and are shown by vertical bars. Most of the energy in the staccatos is below 1,000 cps, with the relative intensity shown by the relative blackness of the bars. These sounds were probably made by a squirrelfish. They are similar to staccatos reported by WINN (1964) for the squirrelfish *Holocentrus rufus*. The horizontal lines in Figure 7, especially prominent near 400 and 800 cps, were caused by the inverter associated with the gyroscope. Had a directional hydrophone been employed, this undesired signal would have been largely eliminated.

Variable-interval sounds, typical of those made by triggerfish, were also recorded. They were a series of knock-like sounds approximately 1·5 to 4·0 seconds apart and 0·5 second long, with frequencies between 200 and 800 cps. No sounds made by snapping shrimp were obtained, although these shrimp occurred on the adjacent inshore reef.

Incidental ichthyological studies

Although not a programmed mission, a great many observations were made on noncommercial fishes. These incidental observations have been tabulated as Appendix Table 1. An analysis of these records throws new light on our

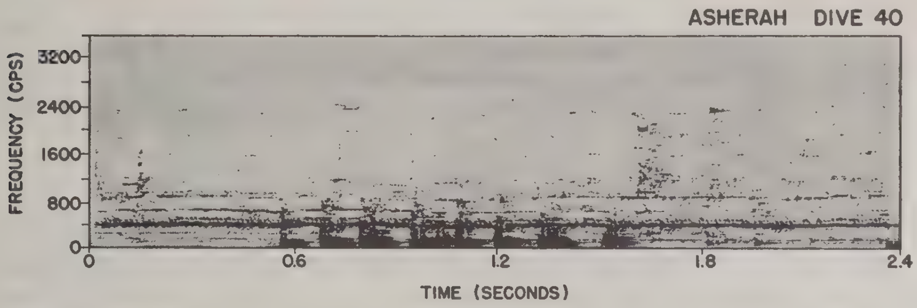

Figure 7. Spectogram of a fixed-interval staccato sound, probably made by a squirrelfish (Holocentridae).

concepts of the Hawaiian fish fauna and on the biology of tropical marine fishes. It is unfortunate that, except for *Holocentrus lacteoguttatus*, no fish specimens could be captured from the submarine. This lack was partly remedied by rod-and-reel fishing in the diving area from the "Townsend Cromwell". The specimens captured provided meristic data impossible to obtain from within the submarine. The reliability of the sight identifications may still be questioned, although every effort was made to eliminate dubious records from our data.

Over 100 fish species were seen on the 50 "Asherah" dives. These were distributed among 41 fish families, with the Chaetodontidae, Acanthuridae, Holocentridae, Carangidae, and Labridae having the greatest numbers of species. In terms of the numbers occurring at various depths, it must be remembered that some depths were studied more exhaustively than others. The depth categories of 0 to 30 m and 183 to 192 m were inadequately sampled. The number of fish species seen throughout "Asherah's" diving range was as follows:

Depth range (m)	No. of species
0– 30	23
31– 60	80
61– 91	57
92–121	55
122–152	33
153–182	22
183–192	15

A remarkable feature was the occurrence of typical "shallow-water" fishes in the greater depths. The following species were selected from Appendix Table 1 to illustrate this point. They would ordinarily be regarded as inshore residents (GOSLINE and BROCK, 1960), although a hint of the great depth range of certain ones might be deduced from their capture by dredge (GOSLINE, 1965). Dredging, however, leaves an element of doubt as to the capture depth, because the dredge is lowered and raised with its mouth open.

Species	Observed depth range (m)
Caranx melampygus	46–140
Chaetodon lunula	30–158
Chaetodon miliaris	15–183
Gymnothorax sp.	61–192

Species	Observed depth range (m)
Heniochus acuminatus	24–183
Holocentrus lacteoguttatus	101–183
Labroides phthirophagus	24– 91
Melichthys vidua	34–140
Parupeneus multifasciatus	21–140
Parupeneus porphyreus	55–140
Zanclus canescens	21–183

About 35 to 40% of the fish seen deeper than 150 m could have been termed inshore reef species.

Discussion

Not only did we acquire submarine-operating experience with "Asherah", but we also obtained valuable scientific information. Of greatest immediate interest are the observations on the vertical distribution of skipjack tuna and little tunny, about which little is known. The discovery of enormous schools of forage fish in deep water offers an explanation for the occurrence of tuna and other predators there, and simultaneously poses tantalizing questions concerning harvesting the small fish for man's needs. Similar queries arise for the beds of lobsters, pen shells, red coral, and possibly heart urchins. In general, we were surprised at the extent of the deep-water resources.

The "Asherah" discoveries raise a host of questions. How are the schools of small fish and the beds of shellfish nourished? What is the nutritional role of the settling white particles which were encountered so often? Are the adjacent depths regularly used as nursery grounds by reef species? How deep does the inshore fauna extend? This last question has interesting zoogeographical implications, for if the inshore fishes also exist in the depths, they may have used the tops of seamounts as stepping stones on their original journeys to Hawaii.

These questions and problems have affected the Bureau's submarine-development plans. More must be learned about the vertical distribution of tuna before the depth capability of our large research submarine is decided. It is desirable to collect samples of the various animals observed for identification, food analysis, and harvesting studies. Additional data are needed on the environment in the habitats of the various species.

These criteria have been kept in mind in planning another submarine operation in 1967. The vehicle to be chartered must dive to 365 m and have a speed of at least 7·3 km per hr. It must have a manipulator arm and a receptacle for holding the collected specimens, some of which may be motile. Lighting is very important in the depths which are to be visited. We wish to measure as many oceanographic variables as possible. At this time several small submarines with the necessary qualifications are available. The planned operation therefore shows indications of being both interesting and successful.

Acknowledgements

Several staff members of the Honolulu Laboratory offered their observations made from "Asherah" for inclusion in this report; their aid is gratefully acknowledged. The officers and crew of the "Townsend Cromwell" and the operators of "Asherah" gave unstintingly of their time and services to make the Bureau's first submarine venture highly rewarding. Special thanks go to Captain ROBERT E. K. D. LEE of the "Townsend Cromwell", and Mr. ALBERT STOVER, the pilot of "Asherah".

Summary

The Bureau of Commercial Fisheries has determined that a submarine could be a highly useful tool for fishery and oceanographic research. Plans for a nuclear research submarine have been developed, and a programme of testing small submarines has been started. A one-month trial with the two-man submarine "Asherah" is described, and results are evaluated from the standpoints of operations, missions, and scientific findings.

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Appendix

Table 1. Fishes seen on "Asherah" dives

Family/genus and species	No. of dives on which seen	Length range (cm)	Depth range (m)
Carcharhinidae			
Carcharhinus menisorrah (?)	4	90–150	46–116
Dasyatidae			
Dasyatis sp.	5	60–120	79–122
Albulidae			
Albula vulpes	2	40	30– 46
Synodontidae			
Synodus variegatus	1	15	30
Trachinocephalus myops	1	20– 25	30
Unidentified synodontid	1	20	64

Table 1 (continued)

Family/genus and species	No. of dives on which seen	Length range (cm)	Depth range (m)
Myctophidae			
Unidentified myctophids	2	5– 10	94–183
Paralepididae			
Unidentified paralepidids	8	15	40–104
Muraenidae			
Gymnothorax pictus	1	90	30– 46
Gymnothorax sp.	18	90–180	61–192
Congridae			
Unidentified congrids	2	10– 12	88–119
Belonidae			
Ablennes hians	1	75	30
Fistulariidae			
Fistularia petimba	3	40	52– 73
Aulostomidae			
Aulostomus chinensis	6	15– 75	55–113
Holocentridae			
Holocentrus ensifer	4	18– 30	101–110
Holocentrus lacteoguttatus	11	2·5– 15	101–183
Holocentrus scythrops	2	25	30–146
Holocentrus spinifer	3	25– 38	61–110
Holocentrus tiere	2	30	146–183
Holocentrus xanthopterus	1	10– 15	30
Holocentrus sp.	7	15– 20	52–192
Myripristis argyromus	2	30	30– 52
Myripristis berndti	1	10	30
Myripristis chryseres	5	15– 20	101–171
Myripristis sp.	7	25	55–110
Family (?)			
Guppy-like forage	22	2·5– 7	107–192
Serranid-like forage	2	8	171–183
Eleotrid-like forage	5	5– 8	116–183
Bothidae			
Bothus pantherinus	1	15– 25	30
Unidentified bothid	1	10	30– 37
Sphyraenidae			
Sphyraena sp.	1	90	61
Serranidae			
Caesioperca thompsoni	4	10– 15	55–110
Odontanthias elizabethae	3	8– 15	165–177
Odontanthias fuscipinnis	1	8– 10	192
Unidentified Anthiinae	1	–	158
Priacanthidae			
Priacanthus cruentatus	2	25– 35	30–137
Apogonidae			
Apogon sp. (dark band)	2	10	110–116
Apogon sp. (no dark band)	5	–	79–192
Malacanthidae			
Malacanthus hoedtii	2	18– 25	40– 61
Carangidae			
Carangoides ajax	1	100–120	61
Carangoides ferdau	4	30	30– 67
Caranx melampygus	6	45– 60	46–140
Caranx sp.	16	20– 75	40–137
Decapterus pinnulatus	10	20– 25	15–110
Scomberoides sanctipetri	1	60	30
Seriola aureovittata	2	45– 60	101–107
Seriola sp.	11	40– 90	61–158
Trachurops crumenophthalmus	3	25	1–110

Table 1 (continued)

Family/genus and species	No. of dives on which seen	Length range (cm)	Depth range (m)
Lutjanidae			
Aprion virescens	4	60–90	46– 67
Etelis carbunculus	2	75–90	134–158
Etelis marshi	4	45–90	116–174
Pristipomoides microlepis	1	25–30	30
Pristipomoides sp.	2	30–75	101–140
Rooseveltia brighami	1	20	110
Mullidae			
Mulloidichthys auriflamma	1	20–25	30– 46
Mulloidichthys pflugeri	2	30–50	30–110
Parupeneus chryserydros	1	–	30– 46
Parupeneus multifasciatus	11	10–30	21–140
Parupeneus pleurostigma	1	10–15	30– 46
Parupeneus porphyreus	3	15–50	55–140
Sparidae			
Monotaxis grandoculis	3	30–60	61–101
Kyphosidae			
Kyphosus cinerascens	1	20–25	85
Chaetodontidae			
Centropyge potteri	3	8	21– 55
Chaetodon corallicola	2	8	46– 61
Chaetodon fremblii	2	10	55– 61
Chaetodon lineolatus	4	10	110–171
Chaetodon lunula	4	12	30–158
Chaetodon miliaris	24	10–15	15–183
Chaetodon multicinctus	2	8	15– 46
Chaetodon sp.	2	8–15	104–162
Forcipiger longirostris	6	8–10	30– 61
Hemitaurichthys zoster	1	10	24– 30
Heniochus acuminatus	13	8–18	24–183
Holacanthus arcuatus	13	8–18	30–131
Histiopteridae			
Histiopterus typus	1	18	183
Cirrhitidae			
Paracirrhites arcatus	1	8–10	24–300
Pomacentridae			
Chromis leucurus	2	8	24– 55
Chromis verater	15	10–18	21– 14
Dascyllus albisella	3	8–10	24– 46
Labridae			
Bodianus bilunulatus	5	20–50	30–110
Cheilinus rhodochrous	2	–	30– 91
Coris flavovittata	3	25–40	30– 61
Coris gaimardi	2	–	21– 46
Cymolutes leclusei	1	18	30
Iniistius pavoninus	1	20	30
Labroides phthirophagus	6	5–8	24– 91
Pseudocheilinus tetrataenia	2	5	24– 61
Thalassoma duperreyi	1	–	15– 21
Scaridae			
Unidentified scarids	8	60–120	30–104
Zanclidae			
Zanclus canescens	12	15– 20	21–183
Acanthuridae			
Acanthurus dussumieri	4	20	30–128
Acanthurus glaucopareius	2	10–15	49– 67
Acanthurus leucopareius	1	–	85
Acanthurus olivaceus	5	20	34– 46
Acanthurus sandvicensis	1	10	30– 46

Table 1 (continued)

Family/genus and species	No. of dives on which seen	Length range (cm)	Depth range (m)
Acanthurus xanthopterus	7	35–45	46– 91
Ctenochaetus strigosus	1	–	30– 46
Naso brevirostris	1	25	30– 46
Naso hexacanthus	14	30–45	15–137
Naso lituratus	2	–	49– 61
Zebrasoma flavescens	1	–	30– 46
Scombridae			
Acanthocybium solandri	2	–	91–183
Euthynnus affinis	1	–	116
Katsuwonus pelamis	2	45	122–137
E. affinis or *K. pelamis*	3	45	98–152
Gobiidae			
Unidentified gobiids	2	10	61–183
Blenniidae			
Runula ewaensis	1	10	55
Runula sp.	1	10	24– 30
Scorpaenidae			
Unidentified scorpaenids	3	2–10	94–177
Dactylopteridae			
Dactyloptera orientalis	1	25	30
Balistidae			
Balistes bursa	5	5–35	30–101
Balistes capistratus	9	8–30	15–107
Canthidermis maculatus	2	20–30	116–122
Melichthys vidua	19	15–35	34–140
Xanthichthys ringens	8	12–20	30– 64
Unidentified balistids	8	–	38–192
Monacanthidae			
Alutera monoceros	1	40	30
Alutera scripta	2	60	85–116
Amanses albopunctatus	1	20	30
Pervagor spilosoma	3	8–15	24– 46
Tetraodontidae			
Lagocephalus hypselogeneion	1	15–20	30
Canthigasteridae			
Canthigaster cinctus	4	8	15– 55
Diodontidae			
Diodon hystrix	2	20–25	24– 46

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RISSO DOLPHIN IN WASHINGTON STATE

On 20 April 1967, Paul Iwanaga and I found the carcass of a young male Risso dolphin, *Grampus griseus* (Cuvier), on the beach at Makkaw Bay (48°19′N, 124°40′W), 5 mi. SW Neah Bay, Washington. Only one other specimen is known from the Pacific Coast of North America north of California; it was shot by a fisherman on the west side of Stuart Island, British Columbia (Guiguet and Pike, Murrelet, 46: 16, 1965).

According to a resident, the carcass had been on the beach about 1 month. Although the skin had sloughed off, the scratch-like marks, typical of this species, could be seen in the blubber layer as reddish streaks about 1 inch wide. The light gray of the head could also be seen faintly despite the "sunburned" appearance of the exposed left side. A .22 caliber bullet lodged in the gum line of the lower jaw had apparently entered from the top of the head near the blowhole.

TABLE 1.—*Measurements of* Grampus griseus *(MMBL 3769). Where applicable, body measurements are in a straight line.*

Snout to notch of flukes	258 cm
Snout to insertion of flipper	42 cm
Notch of flukes to umbilicus	152 cm
Notch of flukes to genital aperture	112 cm
Notch of flukes to anus	88 cm
Length of base of dorsal fin	46 cm
Anterior edge of flipper	43 cm
Posterior edge of flipper	33 cm
Maximum width of flipper	14 cm
Span of flukes	46 cm
Width of flukes	14 cm
Maximum girth (103 cm from tip of snout)	150 cm
Girth behind flippers	142 cm
Greatest length of skull	477 mm
Greatest (squamosal) breadth of skull	315 mm
Length of rostrum	233 mm
Breadth of rostrum at level of antorbital notches	183 mm
Length of right mandible	391 mm
Length of mandibular symphysis	53 mm
Greatest height of right mandible	111 mm
Alveolar length of right toothrow	72 mm
Alveolar length of left toothrow	84 mm

TABLE 2.—*Stomach contents of* Grampus griseus *(MMBL 3769).*

Food item	Number of individuals represented
Onychoteuthis banksii (beak)	1
Octopodoteuthis sicula (beak and fragments)	1
Chiroteuthis veranyi (beaks and buccal masses)	16
Gonatus fabricii (beaks and buccal masses)	4
Gonatidae[1]—form "A" (beaks)	7
Gonatidae[1]—form "B" (beaks)	13
Unidentified (beaks)	2

[1] Not *Gonatus fabricii.*

Body measurements are presented in Table 1. The tip of the dorsal fin, eyes, blowhole, ear holes, and the areas surrounding them were damaged by gulls and crows and could not be measured accurately. The specimen is considerably smaller than one reported from California (Orr, J. Mamm., 47: 341–343, 1966). Orr's specimen was 325 cm total length; mine was 258 cm.

There are five teeth in the right mandible, six in the left; all protrude above the gum. I sectioned the third right tooth longitudinally and counted three complete dentin layers (annual?) and a fraction of a fourth. External rings could be correlated with the dentin layers. Alveolar lengths of the toothrows are given in Table 1.

Sixty-nine vertebrae include seven cervical (first six fused), 13 thoracic, 19 lumbar, and 30 caudal. Fusion of the vertebral epiphyses is not complete. Eighteen chevron bones are present. There are 13 pairs of ribs; the posterior pair is floating, the anterior six pairs are double-headed. I counted the phalanges of the right flipper with the aid of a radiograph. The first digit has two areas of ossification or phalanges, the second has 10, the third has eight, the fourth has four, and the fifth has two.

The right testis measured 125 mm long and 20 mm in greatest diameter; it weighed 30.4 g. The left testis was 120 mm, 20 mm, and 29.2 g. The lengths of the pelvic bones are 72 mm (right) and 70 mm (left).

I examined the stomach in the field and saved the contents for identification. No parasites or fish remains were found. Fifty grams of squid beaks and fragments were identified by Clifford H. Fiscus. Represented were 44 individuals of at least seven different groups (Table 2).—RICHARD K. STROUD, *Bureau of Commercial Fisheries, Marine Mammal Biological Laboratory, Seattle, Washington.* *Accepted 6 November 1967.*

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*Commercial Values of Estuarine-Generated Fisheries on the South Atlantic & Gulf of Mexico Coasts** †

ABSTRACT

A series of reports was designed for this Symposium to illustrate the extent and value of natural resources directly related to marshes and estuaries. This report deals specifically with the commercial importance of estuarine finfishes in the Gulf of Mexico and South Atlantic section of the United States.

Some of the significance of estuaries in perpetuating portions of the marine resource has been proven by research and catch statistics. Scientific documentation from a number of researchers and agencies shows that, depending upon geographical area, 65 to 90 per cent of the commercial catch of finfish in the United States consists of estuarine-dependent species. It can be conservatively estimated that in 1965 the catch of estuarine-dependent finfish in Southeastern United States amounted to 1.1 billion pounds having an ex-vessel value of $32 million.

The world demand for animal protein is steadily increasing, and species of marine fish—particularly clupeoids—are becoming progressively more important in supplying that need. Clupeoid fishes caught in the United States are estuarine dependent and are harvested largely for their value as protein supplement in diets of domestic animals. The usefulness of the rich coastal zone to man will be more accurately reflected when the untapped potential among these fishes is developed more extensively. Preparation is being made for a new fishery in the Gulf of Mexico for one of these species, the thread herring (**Opisthonema oglinum**).

This report was written as one of a series in the Marsh and Estuary Management Symposium to present the values of commercially harvestable species of finfish living in or in some way dependent on the estuarine zone of the Gulf of Mexico and South Atlantic region. Preparation of such a report is uncomplicated in a sense because commercial catches and values of estuarine-oriented species in this section of the Nation are recorded, published, and readily available. From another viewpoint, however, untapped resources and their application to solution of growing food problems of the world must be considered, although briefly, to insure that the full significance of those species for human nutrition is recognized.

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*JAMES E. SYKES, *Director*, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida.

†Contribution No. 35, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida.

Biological investigations have proven that commercial fisheries on the continental shelf of the United States are largely for species which spend a portion of their lives in estuaries. McHugh (1966) stated that nearly two-thirds of the total catch of fish and shellfish from waters of the east coast of the United States and well over half of the entire U. S. commercial catch is made up of estuarine-dependent species. Skud and Wilson (1960) stated that estuarine-dependent species such as shrimp, menhaden, and oysters dominate the Gulf of Mexico fishery and account for about 90 per cent of the annual value of the fisheries. Sykes and Finucane (1964) found that the top 23 species in Gulf of Mexico commercial fisheries occurred as juveniles in Tampa Bay, Florida. Twenty of the species were finfishes. For the South Atlantic and Gulf fisheries, an estimate of 75 per cent of the commercial catch of finfishes is composed of species dependent on estuaries appears to be reasonable, even conservative. In 1965 the commercial catch of all finfish in that area amounted to 1.48 billion pounds worth $42 million. The estimated catch of estuarine-dependent finfish (75 per cent) therefore amounted to 1.1 billion pounds worth about $32 million and constituted 28 per cent of the Nation's commercial catch of all finfish.

These and similar statistics have convinced research scientists, managers, and laymen that estuaries are essential to fish production and therefore deserve more careful attention than they have received in the past. As a guide for management, the Gulf States and the Bureau of Commercial Fisheries are now cooperatively investing considerable amounts of effort and money in a descriptive, hydrological, sedimentological, and biological inventory of Gulf estuaries. Commercial fisheries and their estuarine environment represent the main subject of the studies that will result in a series of atlases designed to provide a portion of the base-line data necessary for the future management of estuaries. A policy statement of the Atlantic States Marine Fisheries Commission recently expressed the need for increased emphasis on estuarine research, inventory, and management. Under Public Law 88-309, a sum of $1.5 million is being administered annually (Bureau of Commercial Fisheries and States) in South Atlantic and Gulf States to investigate and to increase the yield of commercial fisheries of estuaries and contiguous waters.

In addition to the efforts of 10 Federal biological laboratories in the South Atlantic and Gulf region, at least 25 state and university laboratories are engaged in some form of estuarine research, much of it related to commercially important finfish. Even this amount of talent, equipment, and money has not yet been able to come abreast of demands for solutions to estuarine management problems. The reasons are simply defined: scientific programs have not generally become attuned to common goals, and the attention to estuarine ecological research is too new to have become maximally effective.

RELATION OF ESTUARINE FISHES TO THE PROTEIN DEMAND

Are estuarine-dependent commercial fisheries important enough to warrant the present attention, or should even greater emphasis be placed upon them, as some of us reason? Replies to those two questions may be found in a report of the President's Science Advisory Committee (1966) which states, "The total demand for animal protein by the world's population cannot be met adequately for many years, probably not until the turn of the century when, it would be hoped, the world's population will have been stabilized and agricultural and aquicultural technology will have had an opportunity to catch up. We cannot expect to close this gap unless we begin now." Economists of the Bureau of Commercial Fisheries project that demand or consumption of edible fish and shellfish products, which was 5.0 billion pounds in 1966, will reach 5.9, 7.8, and 12.0 billion pounds in 1973, 1985, and 2000, respectively. Utilization of fish for industrial purposes was 7.0 billion pounds in 1966 and is expected to reach 10.2, 12.8, and 16.1 billion pounds in 1973, 1985, and 2000, respectively. Those of us engaged in investigating commercial fisheries believe that a significant part of the food demand can be met by intensive utilization and cultivation of estuarine resources.

Although exploration of fishes in the ocean depths will no doubt lead to the discovery of large quantities of additional protein for human consumption, perhaps research coupled with the wise use of the coastal zone, or more specifically of the highly fertile estuary, will lead to greater achievements in augmenting the needed supply of food. Walford (in press) stated that "In spite of all the talk in recent years about the potential food in the sea, the vast majority of species which are utilizable and which can be economically harvested are closely associated with land masses." The estuary is more controllable or "farmable" than the deeper environment. Any increase in pounds of protein per unit area through man's efforts—excluding the sophistication of offshore fishing techniques—is likely to come from the nearshore zone. Moreover, the capability so necessary for deep-water work can be developed more easily by shifting effort progressively from the coastal zone toward the deeper zone.

PRESENT AND FUTURE IMPORTANCE OF SOME PELAGIC SCHOOLING SPECIES THAT ARE ESTUARINE DEPENDENT

In our consideration of present and future protein needs of the world, we see that a great part of the solution lies within species of fish generated by the estuarine zone. Chapman (1967) has noted that the trend in world fish catches shows an increase in herring-like or clupeoid fishes from one-quarter of the catches in 1948 to about one-half in 1965. He stated that the reasons for the increase in catches of herring-like fishes are: (1) There are more of them in the ocean than any other kind of animal presently harvested, (2) they aggregate in large schools which can be efficiently and cheaply caught, and (3) animal husbandry practices in the past 20 years have been revolutionized by adding animal protein supplements, primarily fish meal, to the diets of domestic fowl and mammals.

The bulk of the herring-like fishes that make up half of the world's catches are estuarine dependent. Among them, two species of menhaden, **Brevoortia tyrannus** and **B. patronus**, constituted the largest catch ever landed in the United States (2.3 billion pounds in 1962). Recently great concern has been expressed over a progressive decline in menhaden landings; nevertheless, in 1965 menhaden accounted for 36 per cent of the entire U. S. catch (Bureau of Commercial Fisheries, 1967).

Reintjes and Pacheco (1966) stated that the association of menhaden with estuaries for the greater part of the first year of life appears to be a persistent, if not a necessary aspect of the life history. The adults spawn in oceanic waters of the continental shelf and the larvae subsequently enter the estuary where metamorphosis and growth occur. These authors stated that the physical, chemical, and biological factors of the estuarine environment affect and in some way determine the populations of menhaden. The value of a Gulf or South Atlantic estuary is therefore reflected in part by species of menhaden which constitute such a large portion of this Nation's catches and contribute heavily to human nutritions by serving as an animal protein supplement.

Although there is reason for concern when such an important fishery begins to decline, there are obviously large untapped resources to ease the effects of the loss—again, estuarine-dependent species—on the U. S. continental shelf and especially in the Gulf of Mexico. Domestic fish meal production needs to be expanded far beyond that of any past period. The Bureau of Commercial Fisheries is aware of the growing need for fish protein; its exploratory research has led to estimates that stocks of other clupeoids and pelagic species are available in the Gulf of Mexico in magnitude at least as great as the menhaden, which has yielded an annual average of about 1 billion pounds. The available and untapped stocks include Spanish sardines (**Sardinella anchovia**), scaled sardines (**Harengula pensacolae**), bumpers (**Chloroscombrus chrysurus**), and scad (**Decapterus** sp.), but are predominantly thread herring (**Opisthonema oglinum**).

Butler (1961) reported that the range of thread herring extends from the Gulf of Maine to Rio de Janeiro, that it is very abundant from North Carolina to the West Indies, and that heavy concentrations occur between Cape San Blas and Key West, Florida. Our observations of experimental commercial fishing for thread herring on the Florida Gulf Coast (1965) and those of Butler for 1958-60 showed the resource to be possibly capable of supplying a minimum annual catch of 1 billion pounds. Catches ranged as high as 27 tons per set of a lampara net in the winter of 1958-59, and from 5 to 40 tons per set of a purse net in 1959-60. Landings amounted to 1,400 tons in about 45 days, according to Butler (1961). Maximum single-set catches of about 50 tons were made near St. Petersburg in 1965. Commercial interests now recognize that a vast amount of protein is available in this resource and are preparing to fish and process thread herring on the west coast of Florida.

MARICULTURE

In addition to the minimal estimate of $195 million worth of fishery products derived presently from U. S. estuaries and the apparent potential for harvest of additional clupeoids, the prospects of successful mariculture should be considered. Estuarine finfish farming has not yet been practiced to any appreciable extent in this Nation although some crude experimentation has taken place. The biological research community is now showing interest in the scientific aspects of increasing the protein supply from estuaries. Berry and Iverson (1967) have noted that successful techniques for culturing marine organisms have yet to be developed, and the introduction of these techniques wil largely depend on adequate knowledge of the biology of the organisms concerned—their tolerances and needs.

Apparently one of the most promising species for beginning studies of finfish mariculture in Gulf and South Atlantic estuaries is the pompano **(Trachinotus carolinus).** This fish is readily available in young stages for transport from outer estuarine beaches to enclosed lagoons, shows suitability for farming (indicated by partial success under the hitherto crude methods), grows rapidly, and demands a high price on the market. Fishery scientists are testing the feasibility of growing this species on a commercial basis in at least three areas of Florida and one area in Louisiana. A commercial animal- food company is supplying special diets and acting as a consultant in a project of the Bureau of Commercial Fisheries, St. Petersburg, Florida, which attempts to satisfy nutritional requirements optimally.

No doubt the rearing and marketing of pompano and other marine finfish wil be fraught with many difficulties and failures before a high degree of success can be achieved. The idea holds enough promise, however, to be worth the experimental studies. Should success be obtained, fish farming will represent one more set of values derived from the estuary.

The commercial value of estuarine finfish is significant in the Nation's economy; these fish also supply an essential part of the Nation's protein requirements. In other parts of the world estuarine-dependent fish contribute even more heavily to national economy and food supply. In the future, if predictions are correct, the world population will rely progressively more on food from the sea. We in the United States must not be so shortsighted that we fail to develop methods for the wise use of finfish resources which occupy that portion of the estuary between the headlands and which migrate and school on the continental shelf.

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Fishes of the St. Johns River, Florida

MARLIN E. TAGATZ

THE St. Johns River watershed has an area of approximately 8,350 square miles. The headwaters are about 50 miles north of Lake Okeechobee and 15 miles inland from Florida's east coast. From there, the river flows northward 260 miles to the vicinity of Jacksonville, and then swings eastward for about 25 miles before emptying into the Atlantic Ocean. Tidal influence extends as far upstream as Lake George, 115 miles above the mouth. Salinity varies greatly in the lower reaches, but south of Jacksonville it is normally less than 1 o/oo.

This system is of particular interest because of the extent to which marine forms penetrate the strictly fresh waters in the river's upper reaches. Such fishes as *Archosargus probatocephalus, Sciaenops ocellata, Micropogon undulatus, Pogonias cromis, Lutjanus griseus,* and *Dasyatis* sp. have been found far upstream. As a result, the so-called primary-division freshwater fishes, i.e., those fishes that are intolerant of salt water (Myers, 1938, 1951), often occur together with various marine species.

The St. Johns estuary is a nursery area for the young of many marine fishes that spawn in the ocean, and also is a feeding and spawning area for various adult marine fish. Spawning populations in the river consist of species that are anadromous, those that extend their breeding range into the river, and some that have established isolated resident populations in the fresh water.

The abundance of marine fishes beyond the zone of brackish water (salinity of 5 o/oo or less) probably is due to the configuration of the river and to the presence of moderate traces of salt in its upper reaches. Many tributary creeks and large coves along the lower 25 miles of river provide areas of intermediate salinity where fish can undergo gradual transition from salt to fresh water. Odum (1953) stated that the main reasons for the extensive movement of marine forms into the St. Johns system appear to be the abundance of calcium chloride in the water and the presence of the salt springs that drain into the river. Salinity actually increases with distance upstream between Palatka and Lake George from the discharge of a number of these springs (Beck, 1965).

The boundary between brackish and fresh water, which moves back and forth from its usual location in southern Jacksonville, determines the upstream or downstream penetration of many species. The following selected salinity readings indicate the effect of tidal stage and runoff on the vertical and horizontal location of brackish waters. In October, at low tide, salinity in the channel, 29 miles upstream, was 0 o/oo at the surface and 4.6 o/oo at the bottom; at high tide, it was 10.2 o/oo at the surface and 10.9 o/oo at the bottom. Salinity on the channel bottom normally is greater than that at the surface. Freshwater fishes rarely occur downstream of the boundary between brackish and fresh water, and, conversely, marine forms that cannot tolerate fresh water seldom occur upstream of the boundary. For example, *Ictalurus catus* and *I. punctatus* were the only freshwater forms collected at salinities above 1 o/oo (up to 9 o/oo).

The abundance and size of many fishes changes seasonally with temperature. Gunter (1945) stated that the temperature cycle was more definite than general salinity changes and was chiefly responsible for the seasonal movements and other recurrent activities of marine fishes in Texas. The occurrence in the St. Johns of marine forms that reach the northern or southern limit of their ranges off northeast Florida is particularly dependent on favorable seasonal temperatures.

Various scientists have contributed to knowledge of the fish fauna of the St. Johns River, particularly since the turn of the century. The first comprehensive checklist of Florida fishes included 112 species from the St. Johns, of which 28 were found only at the mouth (Evermann and Kendall, 1900). Fowler (1945) included a number of records from the system in his study of fishes of the southern Piedmont and Coastal Plain. The most extensive study was a 10-year investigation by McLane (1955), who provided an annotated list of the species known to occur in the St. Johns drainage, but excluded those forms found only near the mouth. Of the 118 forms he reported, 52 are strictly freshwater species. Some of McLane's data (collected in 1953) were from a long-term study of the exploited fish populations of the river (Moody, 1961). Carr and Goin (1959) reported the occurrence of certain marine species in the St. Johns in their guide to the freshwater fishes of Florida. Briggs (1958) summarized the ranges of St. Johns River fishes in his checklist of Florida species.

From April 1961 to November 1963, the seasonal occurrence of fishes in trawl and seine collections was noted during a study of the blue crab (*Callinectes sapidus*) in the St. Johns River by the Bureau of Commercial Fisheries. Capture of fish was incidental to the "random" or regular sampling of juvenile crabs. The number and size range of many of the fish collected from 10 to 135 miles upstream were summarized and a complete checklist was prepared.

A 70-foot seine having a funnel-shaped bag 15 feet long (net, ⅜-inch, and bag, 5/32-inch stretched mesh) and an 8-foot trawl (net, ½-inch, and bag, ¼-inch stretched mesh) were used to obtain nearly all of the fish. Specimens of *Sphyrna lewini* were obtained from commercial fishermen.

At the time of each collection we determined surface salinity in parts per thousand (hydrometer readings corrected for temperature) and surface water temperature in degrees centigrade. All salinity readings beyond 30 miles upstream were less than 1 o/oo and were recorded as 0 o/oo.

Specimens in each sample were identified, counted, and measured in the field. Representative individuals from almost all collections were preserved in 10 per cent formalin and sent to the Florida State Museum, Gainesville, Fla., for identification and inclusion in its collection of fishes. Lengths of fishes with forked tails were measured from the tip of the snout to the caudal fork; those with nonforked tails were measured to the tip of the longest caudal ray. Fork lengths were taken in preference to other measurements because of the ease and speed with which they could be obtained.

COLLECTING LOCALITIES

Collections were obtained from 12 localities or stations that were assigned letters from A to L according to distance upstream (Fig. 1). Fish from tributary streams (stations A, C, E, and F) were captured 1 to 3 miles from the mouth of the tributary. Specimens from the main river and from Lake George (stations B, D, and G to L) were taken in the channel and adjacent waters.

The various stations represented different types of habitat. The bottom material at stations C, E, and F was muck; at all others it was firmer mud and sand. Bottom vegetation was most dense at stations H and I where it consisted of coontail-moss (*Ceratophyllum*

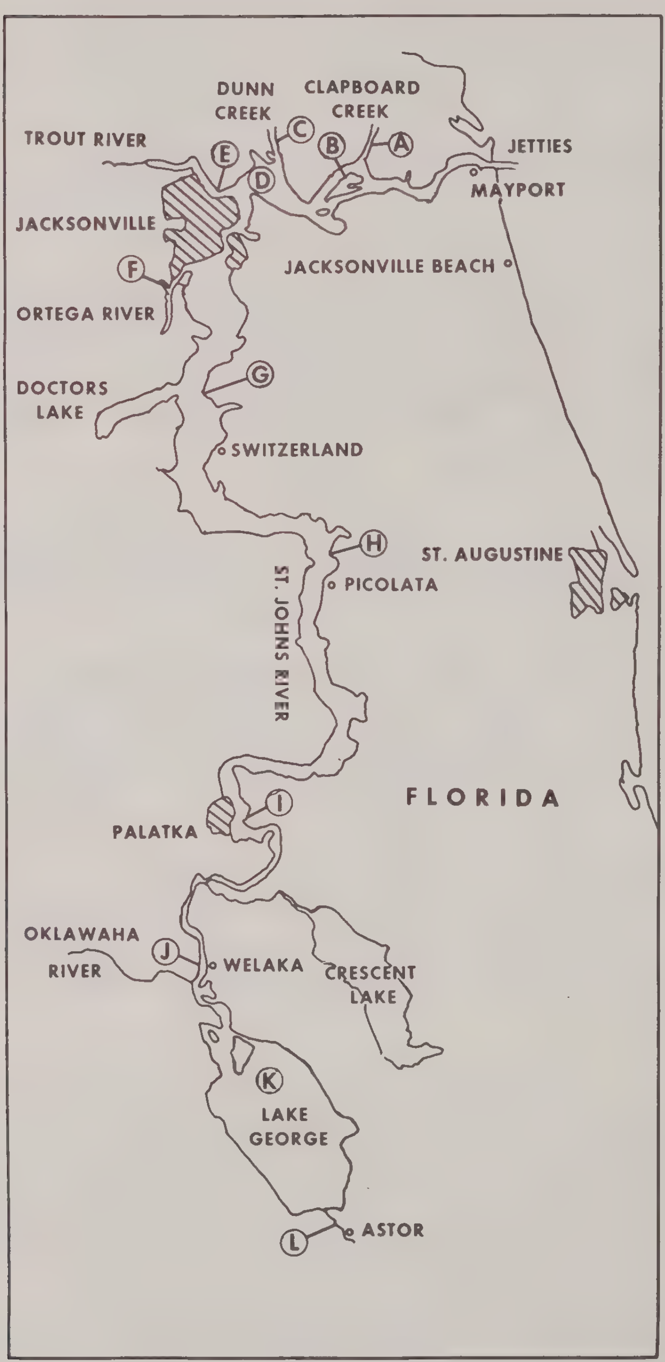
DUNN CREEK
CLAPBOARD CREEK
TROUT RIVER
A
B
C
D
E
JETTIES
MAYPORT
JACKSONVILLE
JACKSONVILLE BEACH
F
ORTEGA RIVER
G
DOCTORS LAKE
SWITZERLAND
H
ST. AUGUSTINE
PICOLATA
ST. JOHNS RIVER
FLORIDA
I
PALATKA
OKLAWAHA RIVER
J
WELAKA
CRESCENT LAKE
K
LAKE GEORGE
L
ASTOR

Fig. 1. Location of the 12 collecting stations, A to L, in the St. Johns River.

sp.) and eelgrass (*Vallisneria* sp.). The maximum depths were 6 feet at station C, 11 feet at F and K, and more than 20 feet at all other stations.

The following is a complete list of collections, numbered consecutively by station and date. Data for each station are given in the order: year, collection number (in parentheses), month and day, surface salinity (o/oo) and surface temperature (° C). Salinity is omitted for stations G to L, where all readings were 0 o/oo.

Station A (10 miles upstream).
1961: (1) April 18—14.6, 20.0; (2) May 17—27.3, 25.2;
(3) June 7—21.5, 28.8
1962: (4) Mar. 13—28.2, 17.4; (5) Mar. 29—20.8, 21.5
(6) Apr. 9—25.8, 19.3; (7) Sept. 19—15.8, 30.0
1963: (8) Feb. 14—7.7, 11.0; (9) Feb. 20—10.8, 13.0;
(10) Mar. 5—9.5, 19.0; (11) Mar. 21—11.4, 18.5;
(12) Apr. 9—22.1, 21.3; (13) Apr. 22—19.5, 27.0;
(14) Apr. 23—15.4, 23.5; (15) May 7—26.8, 23.5;
(16) May 22—23.1, 27.0; (17) June 5—24.7, 26.6;
(18) June 18—22.5, 28.7; (19) July 3—14.5, 27.4;
(20) July 23—14.5, 29.2; (21) Aug. 13—15.8, 29.8;
(22) Aug. 26—20.1, 29.5; (23) Aug. 27—25.2, 28.7;
(24) Sept. 30—10.3, 24.0; (25) Oct. 4—7.9, 26.2;
(26) Nov. 18—13.1, 17.4;

Station B (13 miles upstream)
1962: (1) Mar. 13—28.0, 17.0; (2) May 15—30.2, 26.5;
(3) June 6—23.7, 28.5; (4) Aug. 6—14.1, 30.1;
(5) Sept. 6—16.0, 28.3; (6) Sept. 19—15.8, 30.0
1963: (7) July 23—19.6, 30.0

Station C (20 miles upstream)
1961: (1) Oct. 24—13.4, 22.2; (2) Nov. 20—13.7, 20.3;
(3) Dec. 19—9.0, 19.8
1962: (4) Jan. 15—24.5, 12.8; (5) Feb. 19—22.2, 18.5;
(6) Mar. 29—18.0, 21.5; (7) Apr. 9—20.0, 23.5;
(8) May 25—25.0, 29.5; (9) June 14—19.9, 29.2;
(10) July 12—17.5, 31.4; (11) Aug. 10—0, 30.6;
(12) Aug. 16—14.0, 31.0; (13) Aug. 30—13.7, 30.8;
(14) Sept. 17—10.2, 29.1; (15) Oct. 24—11.1, 21.0;
(16) Nov. 19—8.8, 18.0; (17) Dec. 17—12.0, 12.0;
(18) Dec. 18—10.3, 13.0
1963: (19) Jan. 17—6.9, 14.0; (20) Feb. 14—1.7, 10.5;
(21) Mar. 4—0, 17.5; (22) Mar. 7—0, 16.8;
(23) Mar. 18—5.2, 21.0; (24) Mar. 19—3.9, 25.7;
(25) Apr. 10—10.5, 21.5; (26) Apr. 23—6.7, 23.0;
(27) May 8—21.3, 24.0; (28) May 21—16.6, 26.2;
(29) June 4—22.7, 26.4; (30) June 17—10.3, 28.5;

(31) July 2—0, 27.5; (32) July 23—5.8, 29.1;
(33) Aug. 13—13.3, 31.0; (34) Aug. 26—7.6, 31.5;
(35) Sept. 9—4.0, 28.5; (36) Sept. 30—0, 25.4;
(37) Oct. 8—0, 24.1; (38) Oct. 18—1.0, 23.0;
(39) Nov. 19—2.5, 20.0

Station D (22 miles upstream)
1961: (1) Aug. 16—24.5, 29.0
1962: (2) May 29—13.7, 29.7
1963: (3) Jan. 29—18.3, 11.7

Station E (25 miles upstream)
1961: (1) Apr. 18—5.7, 21.0; (2) May 9—11.3, 24.8;
(3) June 7—14.3, 30.8; (4) Aug. 16—13.5, 28.2;
(5) Oct. 24—9.5, 22.0; (6) Nov. 20—8.8, 20.5;
(7) Dec. 19—10.0, 20.5
1962: (8) Jan. 15—17.8, 14.0; (9) Feb. 19—19.0, 21.2;
(10) Mar. 29—16.9, 18.5; (11) May 25—22.1; 33.8;
(12) June 14—14.9, 29.9; (13) July 12—15.3, 34.1;
(14) July 27—11.0, 30.0; (15) Aug. 10—0, 32.6;
(16) Aug. 16—9.0, 31.8; (17) Sept. 17—8.4, 30.8;
(18) Oct. 24—8.0, 21.0; (19) Nov. 19—5.5, 19.4;
(20) Dec. 17—10.8, 11.0
1963: (21) Jan. 17—5.2, 13.0; (22) Mar. 6—2.0, 19.5;
(23) Mar. 20—3.0, 23.5; (24) Apr. 8—13.9, 20.3;
(25) Apr. 24—6.6, 24.3; (26) May 6—17.9, 22.8;
(27) May 20—14.9, 27.0; (28) June 3—22.1, 26.7;
(29) June 19—11.9, 29.1; (30) July 1—0, 29.8;
(31) July 16—10.5, 30.2; (32) July 24—8.6, 29.3;
(33) Aug. 14—12.2, 29.8; (34) Aug. 27—9.0, 31.0;
(35) Oct. 1—6.2, 24.8; (36) Oct. 9—0, 25.3;
(37) Nov. 20—2.2, 16.5

Station F (30 miles upstream)
1962: (1) May 29—11.9, 32.4

Station G (40 miles upstream)
1961: (1) Apr. 17—20.0; (2) May 8—25.5; (3) June 19—25.0

Station H (60 miles upstream)
1961: (1) Apr. 17—21.0; (2) Apr. 19—21.0; (3) May 8—25.5;
(4) June 16—29.0; (5) Aug. 25—29.5; (6) Oct. 23—24.5;
(7) Nov. 21—20.0; (8) Dec. 13—20.2
1962: (9) Jan. 19—12.0; (10) Feb. 21—19.0; (11) Mar. 28—20.5;
(12) Apr. 20—21.2; (13) May 14—26.8; (14) June 13—28.0;
(15) July 17—29.0; (16) July 30—29.3; (17) Aug. 7—30.5;
(18) Aug. 13—31.6; (19) Aug. 15—34.0; (20) Sept. 14—31.0;
(21) Oct. 19—24.1; (22) Nov. 20—17.7; (23) Dec. 14—8.3
1963: (24) Jan. 23—14.0; (25) Feb. 13—13.0; (26) Mar. 12—20.0;
(27) Mar. 25—20.0; (28) Apr. 11—22.2; (29) Apr. 26—23.8;
(30) May 9—25.0; (31) May 23—28.0; (32) June 14—28.9;
(33) June 24—28.8; (34) July 11—28.4; (35) July 29—29.5;

(36) Aug. 12—30.0; (37) Aug. 28—29.8; (38) Sept. 16—26.0;
(39) Oct. 2—24.5; (40) Oct. 10—23.5; (41) Nov. 21—16.6

Station I (84 miles upstream)
1961: (1) Apr. 20—21.5; (2) May 11—19.0; (3) June 8—29.0;
(4) Aug. 29—28.8; (5) Oct. 12—25.2; (6) Nov. 28—20.8;
(7) Dec. 12—21.1
1962: (8) Jan. 16—12.9; (9) Feb. 12—16.0; (10) Mar. 28—19.7;
(11) Apr. 25—25.8; (12) May 28—30.2; (13) June 13—32.8;
(14) July 30—33.5; (15) Aug. 17—30.0; (16) Sept. 18—29.7;
(17) Sept. 26—30.0; (18) Oct. 12—27.4; (19) Nov. 21—19.0;
(20) Dec. 14—8.8
1963: (21) Jan. 23—15.5

Station J (105 miles upstream)
1961: (1) May 11—22.0; (2) June 22—26.0; (3) Oct. 17—23.0;
(4) Nov. 23—19.9; (5) Dec. 21—17.8
1962: (6) Jan. 12—12.0; (7) Feb. 15—20.5; (8) Dec. 19—12.2

Station K (120 miles upstream)
1961: (1) Apr. 21—20.5; (2) May 12—23.8; (3) June 20—26.5;
(4) July 10—29.0
1962: (5) May 23—29.0

Station L (135 miles upstream)
1961: (1) Apr. 21—21.0; (2) May 12—28.5; (3) June 20—26.8

FISHES

The fish fauna of the St. Johns River consists of 55 species that are typical freshwater forms and 115 that are euryhaline (occur both in sea water and water of moderate to zero salinity). One species, *Cyprinodon hubbsi,* is endemic to the river system. Families particularly well represented are Clupeidae, Cyprinodontidae, Centrarchidae, Sciaenidae, and Gobiidae.

The list of marine fish for the St. Johns would be longer if fish collected in the river within a few miles of the mouth had been included. In this category, I collected *Anchoa lyolepis* (dusky anchovy), *Hippocampus erectus* (spotted seahorse), *Pomatomus saltatrix* (bluefish), and *Sphaeroides spengleri* (bandtail puffer).

The following list is a taxonomic grouping of all records of fish for the St. Johns known to me, 170 species representing 55 families. This listing is primarily based on 116 species reported by McLane (1955) and 51 records from the present study. The changes that were made in the records given by McLane are: *Notropis* sp. to *N. welaka, Ogcocephalus* sp. to *O. cubifrons, Ictalurus platycephalus* to *I. brunneus* (validated by Dr. Ralph Yerger, Florida State University) and deletion of *Alosa pseudoharengus* (a 19th-century record considered in error). The checklist also contains *Paralichthys albigutta* (reported in Carr and Goin, 1959), and, from specimens in the Florida State Museum collection, *Elassoma okefenokee* and *Umbra pygmaea.* Nomenclature follows that of Bailey, Lachner, Lindsey, Robins, Roedel, Scott, and Woods (1960).

For each of the 101 euryhaline species collected in the present study, I have included a summary of the stations (collection number in parentheses) at which it was taken, the ranges in surface salinity and temperature when collected, and number and length range of fish, by month. Salinity is in parts per thousand, water temperature in degrees C, and length (FL) in mm. Some specimens were not identified to species and are listed as undetermined, by genus or family. In addition to *Anchoa hepsetus* and *A. mitchilli,* one other engraulid (of uncertain identity) was collected and is referred to as *Anchoa* sp. Fourteen euryhaline species, those reported for the river but not obtained in this study, are listed with the notation "None captured."

Entered without annotation are the 55 species that are confined to fresh water (indicated by an F). Except for an adult specimen of *Eleotris picta* captured at station H on August 13, 1962 (first record of occurrence in the river) my samples of strictly freshwater forms provided little new information.

Fifty-one species not previously recorded are designated by an asterisk.

Family PETROMYZONTIDAE

Petromyzon marinus Linnaeus. Sea lamprey. None captured.

Family SPHYRNIDAE

Sphyrna lewini (Griffith and Smith). Scalloped hammerhead*. Station: B(3). Salinity 23.7, temperature 28.5. Number and length: June (2, 324-381).

Family DASYATIDAE

Dasyatis americana Hildebrand and Schroeder. Southern stingray. None captured.

Dasyatis sabina (Lesueur). Atlantic stingray. Stations: A(6), B(6, 17, 20), C(7), D(1), E(37), H(12, 16, 22, 38), I(8, 9, 13, 16, 18-21), J(3-6, 8). Salinity 0-25.8, temperature 8.8-32.8. Number and length: Jan. (5, 495-635); Feb. (3, 478-533); Apr. (3, 533-711); June (2, 508-521); July (2, 394-660); Aug. (2, 330-700); Sept. (2, 310-432); Oct. (2, 500-508); Nov. (5, 381-711); Dec. (8, 432-648).

Family ACIPENSERIDAE

Acipenser brevirostrum Lesueur. Shortnose sturgeon. None captured.

Acipenser oxyrhynchus Mitchill. Atlantic sturgeon. None captured.

Family LEPISOSTEIDAE

Lepisosteus osseus (Linnaeus). Longnose gar. F

Lepisosteus platyrhincus DeKay. Florida gar. F

Family AMIIDAE

Amia calva Linnaeus. Bowfin. F

Family ELOPIDAE

Elops saurus Linnaeus. Ladyfish. Stations: A(25), C(33), E(20, 37), H(17), I(12). Salinity 0-13.3, temperature 11.0-31.0. Number and length: May (1, 51); Aug. (3, 198-250); Oct. (1, 305); Nov. (1, 195); Dec. (1, 239).

Megalops atlantica Valenciennes. Tarpon. None captured.

Family CLUPEIDAE

Alosa aestivalis (Mitchill). Blueback herring. Stations: C(7), L(2). Salinity 0-20.0, temperature 23.5-28.5. Number and length: April (1, 28); May (1, 39).

Alosa mediocris (Mitchill). Hickory shad. None captured.

Alosa sapidissima (Wilson). American shad. None captured.

Brevoortia smithi Hildebrand. Yellowfin menhaden. Stations: A(24); D(3). Salinity 10.3-18.3, temperature 11.7-24.0. Number and length: Jan. (2, 201-266); Sept. (15, 228-254).

Brevoortia tyrannus (Latrobe). Atlantic menhaden*. Stations:

A(25), C(13). Salinity 7.9-13.7, temperature 26.2-30.8. Number and length: Aug. (1, 123); Oct. (10, 69-74).

Dorosoma cepedianum (Lesueur). Gizzard shad. Stations: C(22), G(3), H(17, 37), I(5, 6, 8, 9, 12, 15, 20), J(3-7), K(4). Salinity 0, temperature 8.8-30.5. Number and length: Jan (4, 99-121); Feb. (2, 55-64); Mar. (1, 111); May (1, 287); June 2, 75-80); July (9, 25-157); Aug. (12, 90-272); Oct. (10, 31-234); Nov. (8, 115-220); Dec. (16, 68-237).

Dorosoma petenense (Günther). Threadfin shad. None captured.

Harengula pensacolae Goode and Bean. Scaled sardine*. Stations: H(4, 33), I(3, 12), J(2). Salinity 0, temperature 26.0-30.2. Number and length: May (2, 23-27); June (103, 24-46).

Opisthonema oglinum (Lesueur). Atlantic thread herring*. Stations: A(15, 16, 22, 23), B(6), I(20). Salinity 0-26.8, temperature 8.8-30.0. Number and length: May (160, 21-53); Aug. (48, 73-121); Sept. (1, 59); Dec. (2, 73-81).

Undetermined Clupeidae. Stations: A(10, 14, 18, 20), C(7, 21, 25-28, 32-34), E(22-24, 27), I(4). Salinity 0-22.5, temperature 17.5-31.5. Number and length: Mar. (19, 25-125); Apr. (50, 22-97); May (58, 22-59); June (1, 61); July (45, 43-70); Aug. (46, 26-69).

Family ENGRAULIDAE

Anchoa hepsetus (Linnaeus). Striped anchovy. Stations: A(3, 12, 24, 25), B(6), C(3), D(2), E(3, 12). Salinity 7.9-22.1, temperature 19.8-30.8. Number and length: Apr. (1, 94); May (2, 37-45); June (23, 17-62); Sept. (2, 70-74); Oct. (2, 52-71); Dec. (1, 89).

Anchoa mitchilli (Valenciennes). Bay anchovy. Stations: A(2, 3, 7-9, 12, 14-22, 24, 25), B(6), C(1-9, 11-17, 19-22, 24-34, 36-39), E(3, 5-9, 11, 13-17, 21-29, 35, 37), F(1), G(1-3), H(4, 6-9, 11, 15, 19, 23, 27, 28, 33, 35, 37, 40), I(7-11, 14, 15, 20), J(5-7). Salinity 0-27.3, temperature 8.3-34.1. Number and length: Jan. (281, 21-60); Feb. (26, 31-75); Mar. (92, 29-71); Apr. (321, 40-78); May (658, 23-77); June (738, 19-73); July (897, 21-71); Aug. (1,501, 21-83); Sept. (153, 19-62); Oct. (3,189, 10-68); Nov. (119, 22-61); Dec. (63, 27-71).

Anchoa sp.* Station: E(11). Salinity 22.1, temperature 33.8. Number and length: May (1, 37).

Family UMBRIDAE

Umbra pygmaea (DeKay). Eastern mudminnow. F

Family ESOCIDAE

Esox americanus Gmelin. Redfin pickerel. F
Esox niger Lesueur. Chain pickerel. F

Family SYNODONTIDAE

Synodus foetens (Linnaeus). Inshore lizardfish*. Stations: A(1, 15-21, 24, 25), B(6), C(8-10, 29, 36), E(12-14, 28, 29, 35). Salinity 0-26.8, temperature 13.0-34.1. Number and length: Feb. (1, 99); May (13, 39-104); June (73, 36-118); July (26, 37-136); Aug. (1, 49); Sept. (8, 22-63); Oct. (9, 45-83).

Family CYPRINIDAE

Hybopsis harperi (Fowler). Redeye chub. F
Notemigonus crysoleucas (Mitchill). Golden shiner. F
Notropis chalybaeus (Cope). Ironcolor shiner. F
Notropis cummingsae Myers. Dusky shiner. F
Notropis hypselopterus (Günther). Sailfin shiner. F
Notropis maculatus (Hay). Taillight shiner. F
Notropis petersoni Fowler. Coastal shiner. F
Notropis welaka Evermann and Kendall. Bluenose shiner. F
Opsopoeodus emilae Hay. Pugnose minnow. F

Family CATOSTOMIDAE

Erimyzon sucetta (Lacépède). Lake chubsucker. F

Family ARIIDAE

Bagre marinus (Mitchill). Gafftopsail catfish. Station: D(3). salinity 18.3, temperature 11.7. Number and length: Jan (1, 116).

Galeichthys felis (Linnaeus). Sea catfish. Stations: A(1, 6, 7), C(12-14, 17, 25, 27), D(1), E(20). Salinity 10.2-25.8, temperature

11.0-31.0. Number and length: Apr. (7, 86-186); May (1, 112); Aug. (12, 74-187); Sept. (8, 59-103); Dec. (3, 81-91).

Family ICTALURIDAE

Ictalurus brunneus (Jordon). Snail bullhead. F
Ictalurus catus (Linnaeus). White catfish. F
Ictalurus natalis (Lesueur). Yellow bullhead. F
Ictalurus nebulosus (Lesueur). Brown bullhead. F
Ictalurus punctatus (Rafinesque). Channel catfish. F
Noturus gyrinus (Mitchill). Tadpole madtom. F
Noturus leptacanthus Jordan. Speckled madtom. F

Family ANGUILLIDAE

Anguilla rostrata (Lesueur). American eel. Stations: C(30), E(27, 28, 32, 35), G(1), H(1, 6-11, 14, 16, 18, 19, 22, 23, 25-28, 30-33, 35, 36, 38-40, 42), I(1, 7, 8, 21), J(5-6), K(2,4). Salinity 0-22.1, temperature 8.3-34.0. Number and length: Jan. (31, 52-533); Feb. (6, 155-635); Mar. (16, 136-508); Apr. (7, 115-495); May (10, 165-546); June (6, 118-508); July (11, 152-610); Aug. (12, 74-576); Sept. (2, 274-379); Oct. (9, 251-611); Nov. (10, 120-512); Dec. (10, 279-533).

Family BELONIDAE

Strongylura marina (Walbaum). Atlantic needlefish. Stations: A(17, 25), C(31), E(28, 30, 32), H(15, 17, 29), I(17). Salinity 0-24.7, temperature 22.2-30.5. Number and length: Apr. (13, 28-74); June (3, 136-198); July (5, 76-483); Aug. (6, 252-545); Sept. (2, 114-324); Oct. (1, 356).

Family CYPRINODONTIDAE

Cyprinodon hubbsi Carr. Lake Eustis minnow. F

Cyprinodon variegatus Lacépède. Sheapshead minnow. Station: E(30). Salinity 0, temperature 29.8. Number and length: July (2, 19).

Fundulus chrysotus (Günther). Golden topminnow. F

Fundulus cingulatus Valenciennes. Banded topminnow. F

Fundulus confluentus Goode and Bean. Marsh killifish. Stations: A(9), C(16). Salinity 8.8-10.8, temperature 13.0-18.0. Number and length: Feb. (5, 50-56); Nov. (10, 33-53).

Fundulus heteroclitus (Linnaeus). Mummichog. Stations: A(9, 21, 22, 25), C(16, 18, 21, 27-29, 31, 35, 37), E(22-25, 27-31, 33). Salinity 0-22.7, temperature 13.0-30.2. Number and length: Feb. (7, 50-57); Mar. (42, 6-64); Apr. (11, 54-66); May (52, 34-68); June (81, 24-93); July (48, 17-78); Aug. (6, 34-53); Sept. (2, 25-30); Oct. (6, 28-55); Nov. (15, 31-63); Dec. (25, 35-65).

Fundulus majalis (Walbaum). Striped killifish. Station: B(6). Salinity 15.8, temperature 30.0. Number and length: Sept. (2, 75-79).

Fundulus notti (Agassiz). Starhead topminnow. F

Fundulus seminolis Girard. Seminole killifish. F

Fundulus similis (Baird and Girard). Longnose killifish*. Stations: A(9), B(5, 6). Salinity 10.8-16.0, temperature 13.0-30.0. Number and length: Feb. (4, 60-62); Sept. (6, 22-56).

Jordanella floridae Goode and Bean. Flagfish. F

Leptolucania ommata (Jordan). Pygmy killifish. F

Lucania goodei Jordan. Bluefin killifish. F

Lucania parva (Baird and Girard). Rainwater killifish. Station: H(18, 20). Salinity 0, temperature 31.0-31.6. Number and length: Aug. (5, 22-30); Sept. (9, 29-43).

Family POECILIIDAE

Gambusia affinis (Baird and Girard). Mosquitofish. Stations: C(28, 29), H(17). Salinity 0-22.7, temperature 26.2-30.5. Number and length: May (19, 34-40); June (10, 31-43); Aug. (2, 42-43).

Heterandria formosa Agassiz. Least killifish. F

Poecilia latipinna (Lesueur). Sailfin molly. Stations: C(17), E(24). Salinity 12.0-13.9, temperature 12.0-20.3. Number and length: Apr. (1, 38); Dec. (1, 44).

Family GADIDAE

Urophycis floridanus (Bean and Dresel). Southern hake*. Station: A(8, 9). Salinity 7.7-10.8, temperature 11.0-13.0. Number and length: Feb. (9, 34-120).

Urophycis regius (Walbaum). Spotted hake*. Station: A(8, 9). Salinity 7.7-10.8, temperature 11.0-13.0. Number and length: Feb. (8, 36-121).

Family SYNGNATHIDAE

Oostethus lineatus (Kaup). Opossum pipefish. None captured.

Syngnathus fuscus Storer. Northern pipefish*. Station: E(7). Salinity 10.0, temperature 20.5. Number and length: Dec. (1, 108).

Syngnathus louisianae Günther. Chain pipefish. Stations: A(1, 15-17), C(15, 29, 36), E(11, 12, 35, 36). Salinity 0-26.8, temperature 20.0-33.8. Number and length: Apr. (1, 195); May (3, 115-298); June (5, 56-146); Sept. (6, 78-166); Oct. (6, 76-213).

Syngnathus scovelli (Evermann and Kendall). Gulf pipefish. Stations: A(1), C(6), E(9, 11, 22, 25, 37), H(15, 18, 20, 22), I(19), J(8), K(5). Salinity 0-22.1, temperature 12.2-33.8. Number and length: Feb. (2, 56-135); Mar. (13, 88-126); Apr. (4, 64-130); May (2, 70-141); July (2, 77-136); Aug. (5, 77-107); Sept. (3, 113-126); Nov. (5, 81-121); Dec. (6, 71-99).

Undetermined Syngnathidae. Stations: A(3, 14, 19, 25), C(30, 31, 34, 37, 38), E(2, 4, 27-30). Salinity 0-22.1, temperature 23.0-31.5. Number and length: Apr. (1, 68); May (2, 68-126); June (6, 69-156); July (9, 32-157); Aug. (8, 36-179); Oct. (14, 78-156).

Family APHREDODERIDAE

Aphredoderus sayanus (Gilliams). Pirate perch. F

Family CENTROPOMIDAE

Centropomus undecimalis (Bloch). Snook. None captured.

Family SERRANIDAE

Centropristes philadelphicus (Linnaeus). Rock sea bass*. Station: A(8). Salinity 7.7, temperature 11.0. Number and length: Feb. (2, 129-131).

Centropristes striatus (Linnaeus). Black sea bass*. Station: A(8, 11, 17, 19, 21, 26). Salinity 7.7-24.7, temperature 11.0-29.8. Number and length: Feb. (1, 91); Mar. (2, 101-122); June (1, 28); July (3, 38-71); Aug. (1, 176); Nov. (1, 176).

Mycteroperca microlepis (Goode and Bean). Gag*. Station: B(6). Salinity 15.8, temperature 30.0. Number and length: Sept. (1, 182).

Roccus saxatilis (Walbaum). Striped bass. Station: J(1). Salinity 0, temperature 22.0. Number and length: May (1, 46).

Family LUTJANIDAE

Lutjanus analis (Cuvier). Mutton snapper*. Station: E(12). Salinity 14.9, temperature 29.9. Number and length: June (1, 65).

Lutjanus griseus (Linnaeus). Gray snapper. Stations: A(25), C(35-37), E(8, 20, 35-37), H(42). Salinity 0-17.8, temperature 11.0-28.5. Number and length: Jan. (1, 67); Sept. (11, 19-54); Oct. (27, 24-58); Nov. (4, 40-58); Dec. (1, 105).

Family CENTRARCHIDAE

Acantharchus pomotis (Baird). Mud sunfish. F
Centrarchus macropterus (Lacépède). Flier. F
Chaenobryttus gulosus (Cuvier). Warmouth. F
Elassoma evergladei Jordan. Everglades pygmy sunfish. F
Elassoma okefenokee Böhlke. Okefenokee pygmy sunfish. F
Elassoma zonatum Jordan. Banded pygmy sunfish. F
Enneacanthus chaetodon (Baird). Blackbanded sunfish. F
Enneacanthus gloriosus (Holbrook). Bluespotted sunfish. F
Enneacanthus obesus (Girard). Banded sunfish. F
Lepomis auritus (Linnaeus). Redbreast sunfish. F
Lepomis macrochirus Rafinesque. Bluegill. F
Lepomis marginatus (Holbrook). Dollar sunfish. F
Lepomis microlophus (Günther). Redear sunfish. F
Lepomis punctatus (Valenciennes). Spotted sunfish. F
Micropterus salmoides (Lacépède). Largemouth bass. F
Pomoxis nigromaculatus (Lesueur). Black crappie. F

Family PERCIDAE

Etheostoma fusiforme barratti (Holbrook). Scalyhead darter. F
Etheostoma edwini (Hubbs and Cannon). Brown darter. F
Etheostoma nigrum Rafinesque. Johnny darter. F
Percina nigrofasciata (Agassiz). Blackbanded darter. F

Family CARANGIDAE

Caranx hippos (Linnaeus). Crevalle jack. Stations: A(25), B(7), C(28, 32), E(30). Salinity 0-19.6, temperature 26.2-30.0. Number and length: May (5, 33-54); July (5, 38-106); Oct. (1, 47).

Chloroscombrus chrysurus (Linnaeus). Bumper. Stations: A(20, 22), B(6), C(2), E(7). Salinity 10.0-20.1, temperature 20.3-

30.0. Number and length: July (3, 22-52); Aug. (2, 61-67); Sept. (3, 44-48); Nov. (12, 48-65); Dec. (1, 105).

Oligoplites saurus (Bloch and Schneider). Leatherjacket*. Station: B(6). Salinity 15.8, temperature 30.0. Number and length: Sept. (1, 55).

Selene vomer (Linnaeus). Lookdown*. Stations: A(19), E(29, 32, 35). Salinity 6.2-14.5, temperature 24.8-29.3. Number and length: June (1, 59); July (6, 27-76); Oct. (1, 83).

Trachinotus falcatus (Linnaeus). Permit*. Station: E(31). Salinity 10.5, temperature 30.2. Number and length: July (1, 50).

Vomer setapinnis (Mitchill). Atlantic moonfish*. Station: A(20). Salinity 14.5, temperature 29.2. Number and length: July (1, 38).

Family GERRIDAE

Diapterus olisthostomus (Goode and Bean). Irish pompano. Station: C(32, 34-36). Salinity 0-7.6, temperature 25.4-31.5. Number and length: July (2, 26-40); Aug. (2, 40-68); Sept. (16, 24-78).

Diapterus plumieri (Cuvier). Striped mojarra*. Station: C(13, 15). Salinity 11.1-13.7, temperature 21.0-30.8. Number and length: Aug. (2, 71-73); Oct. (3, 63-76).

Eucinostomus argenteus Baird and Girard. Spotfin mojarra. Stations: A(20-22, 24, 25), B(6), C(1, 13, 15, 16, 32, 34, 36, 39), E(11, 12, 14, 17, 18, 31, 32, 36, 37), H(17, 19), I(6, 7). Salinity 0-22.1, temperature 16.5-34.0. Number and length: May (1, 26); June (2, 30-47); July (36, 36-85); Aug. (13, 28-98); Sept. (15, 22-104); Oct. (61, 16-115); Nov. (134, 15-111); Dec. (2, 45-52).

Eucinostomus gula (Quoy and Gaimard). Silver Jenny*. Stations: A(20-22), B(6), C(10), E(13, 31). Salinity 10.5-20.1, temperature 29.2-34.1. Number and length: July (16, 46-83); Aug. (6, 78-100); Sept. (2, 91-103).

Undetermined Gerridae. Stations: A(18, 19), C(2, 3, 37, 38), E(6, 29, 30, 33-35). Salinity 0-22.5, temperature 19.8-31.0. Number and length: June (41, 36-58); July (66, 46-69); Aug. (19, 79-95); Oct. (37, 22-102); Nov. (12, 46-73); Dec. (8, 44-73).

Family POMADASYIDAE

Orthopristis chrysopterus (Linnaeus). Pigfish. Stations: A(15-

17, 24), C(8), E(11-14, 16, 27, 32, 34, 35), H(15). Salinity 0-26.8, temperature 23.5-34.1. Number and length: May (74, 17-54); June (4, 39-69); July (19, 67-97); Aug. (3, 82-113); Sept. (1, 142); Oct. (2, 115-118).

Family SCIAENIDAE

Bairdiella chrysura (Lacépède). Silver perch. Stations: A(2, 3, 7, 9-11, 16-19), C(2, 10, 11, 13, 14, 16, 29, 32, 38), D(3), E(3, 5, 6, 13, 15, 22, 23, 28-30, 34), H(15, 17-20, 37). Salinity 0-27.3, temperature 11.7-34.1. Number and length: Jan. (1, 142); Feb. (1, 81); Mar. (13, 104-137); May (10, 46-100); June (117, 22-97); July (131, 45-124); Aug. (25, 71-122); Sept. (6, 83-91); Oct. (2, 135-141); Nov. (3, 74-91).

Cynoscion nebulosus (Cuvier). Spotted seatrout. Stations: C(15, 32, 34-38), E(18, 22, 35, 36), H(17). Salinity 0-11.1, temperature 19.5-31.5. Number and length: Mar. (3, 97-118); July (4, 64-84); Aug. (13, 13-136); Sept. (56, 15-128); Oct. (87, 19-173).

Cynoscion regalis (Bloch and Schneider). Weakfish*. Stations: A(3, 15), B(4), C(9, 13), E(3). Salinity 13.7-26.8, temperature 23.5-30.8. Number and length: May (2, 31-32); June (13, 23-65); Aug. (5, 143-206).

Leiostomus xanthurus Lacépède. Spot. Stations: A(2, 3, 8, 10-12, 14, 18, 19, 21), C(1-3, 6-11, 13-15, 21-29, 31, 33-38), D(3), E(1, 6, 10, 12-16, 19, 22-31, 33-37), G(1, 2), H(2-4, 6, 10-12, 14-16, 21, 30), I(1-3, 10-12), K(2). Salinity 0-27.3, temperature 11.0-34.1. Number and length: Jan. (9, 124-158); Feb. (508, 20-188); Mar. (2, 186, 17-164); Apr. (1,250, 16-178); May (823, 38-160); June (504, 40-138); July (255, 57-115); Aug. (60, 68-157); Sept. (15, 96-137); Oct. (26, 97-185); Nov. (15, 105-136); Dec. (2, 129-130).

Menticirrhus americanus (Linnaeus). Southern kingfish*. Station: E(35). Salinity 6.2, temperature 24.8. Number and length: Oct. (4, 28-44).

Micropogon undulatus (Linnaeus). Atlantic croaker. Stations: A(1-3, 8-12, 14-16, 18), B(2), C(2-14, 16-22, 24-30, 32-35, 39), D(3), E(1, 3, 6, 9-14, 16, 17, 19-25, 27-29, 31, 33, 37), F(1), G(1-3), H(2-14, 16, 19, 20, 22, 23, 25-38, 40-42), I(1-16, 19-21), J(2, 6, 7), K(3-5), L(1). Salinity 0-30.2, temperature 8.3-34.1. Number and length: Jan. (368, 16-105); Feb. (388, 5-147); Mar. (1,858, 16-162); Apr. (1,711, 17-155); May (1, 110, 16-182); June (1,499, 24-

145); July (395, 59-162); Aug. (268, 78-171); Sept. (13, 123-154); Oct. (92, 27-175); Nov. (220, 11-162); Dec. (392, 17-151).

Pogonias cromis (Linnaeus). Black drum. Stations: A(16), C(4, 17, 22, 26, 27). Salinity 0-24.5, temperature 12.0-27.0. Number and length: Jan. (1, 194); Mar. (2, 181-184); Apr. (1, 194); May (4, 178-203); Dec. (3, 174-195).

Sciaenops ocellata (Linnaeus). Red drum. Stations: A(20), C(29, 39), E(25, 27, 28, 37), H(31). Salinity 0-22.7, temperature 16.5-29.2. Number and length: Apr. (6, 106-129); May (3, 116-164); June (11, 110-160); July (1, 249); Nov. (6, 31-70).

Stellifer lanceolatus (Holbrook). Star drum*. Stations: A(7), C(36), E(3, 20). Salinity 0-15.8, temperature 11.0-30.8. Number and length: June (3, 94-95); Sept. (24, 12-150); Dec. (1, 77).

Family SPARIDAE

Archosargus probatocephalus (Walbaum). Sheepshead. Stations A(8, 12, 15-18, 20-22, 24, 25), C(14), E(6, 11, 13, 18, 24, 28), H(12, 15, 31). Salinity 0-26.8, temperature 11.0-34.1. Number and length: Feb. (1, 95); Apr. (8, 75-258); May (7, 26-181); June (3, 136-190); July (4, 59-166); Aug. (3, 166-194); Sept. (2, 106-195); Oct. (4, 98-216); Nov. (1, 190).

Lagodon rhomboides (Linnaeus). Pinfish. Stations: A(8, 10, 12-14, 16, 19, 20, 25), B(6), C(8-11, 13, 15, 22, 30-32, 34, 38), D(3), E(11-18, 22-33, 35, 37), H(15, 17, 20). Salinity 0-25.0, temperature 11.0-34.1. Number and length: Jan. (1, 94); Feb. (1, 127); Mar. (14, 102-141); Apr. (14, 21-121); May (27, 22-157); June (32, 44-153); July (117, 43-159); Aug. (22, 73-170); Sept. (11, 104-146); Oct. (23, 72-203); Nov. (2, 100-109).

Family EPHIPPIDAE

Chaetodipterus faber (Broussonet). Atlantic spadefish*. Stations: A(3, 21), E(11, 13, 32, 36). Salinity 0-22.1, temperature 25.3-34.1. Number and length: May (2, 15-28); June (1, 98); July (2, 43-58); Aug. (1, 32); Oct. (1, 24).

Family TRICHIURIDAE

Trichiurus lepturus Linnaeus. Atlantic cutlassfish*. Stations: B(3), C(1, 2). Salinity 13.4-23.7, temperature 20.3-28.5. Number and length: June (3, 330-406); Oct. (1, 134); Nov. (1, 325).

Family SCOMBRIDAE

Scomberomorus maculatus (Mitchill). Spanish mackeral*. Stations: A(18), B(6). Salinity 15.8-22.5, temperature 28.7-30.0. Number and length: June (1, 108); Sept. (1, 58).

Family ELEOTRIDAE

Dormitator maculatus (Bloch). Fat sleeper. Station: H(18). Salinity 0, temperature 31.6. Number and length: Aug. (5, 97-126).

Eleotris picta Kner and Steindachner. Spotted sleeper*. F

Family GOBIIDAE

Awaous tajasica (Lichtenstein). River goby. None captured.

Bathygobius soporator (Valenciennes). Frillfin goby. None captured.

Gobioides broussonneti Lacépède. Violet goby*. Stations: B(3, 5), C(22), F(1), G(2). Salinity 0-23.7, temperature 16.8-32.4. Number and length: Mar. (1, 597); May (2, 185-200); June (1, 502); Sept. (3, 381-572).

Gobionellus boleosoma (Jordan and Gilbert). Darter goby. Stations: A(8, 11, 14, 20-22, 25), B(6), C(15-17, 36, 39), E(17, 20, 21, 26, 27, 29, 34-37), H(20). Salinity 0-20.1, temperature 11.0-31.0. Number and length: Jan. (1, 32); Feb. (1, 37); Mar. (5, 20-39); Apr. (5, 32-44); May (3, 42-49); June (1, 43); July (11, 26-37); Aug. (5, 14-39); Sept. (9, 15-36); Oct. (10, 19-38); Nov. (17, 18-40); Dec. (3, 24-28).

Gobionellus gracillimus Ginsburg. Slim goby*. Station: C(29). Salinity 22.7, temperature 26.4. Number and length: June (2, 129-159).

Gobionellus hastatus Girard. Sharptail goby*. Stations: C(17, 35), E(14, 20). Salinity 4.0-12.0, temperature 11.0-30.0. Number and length: July (1, 218); Sept. (1, 84); Dec. (2, 91-178).

Gobionellus shufeldti (Jordan and Evermann). Freshwater goby. Stations: A(10), C(10, 13, 17, 21-27, 31, 34, 36, 37), E(1, 2, 10, 22-26, 30, 37), G(1), H(18, 25, 27, 29), I(7-9, 19). Salinity 0-21.3, temperature 12.0-31.6. Number and length: Jan. (2, 39-91); Feb. (1, 67); Mar. (151, 28-74); Apr. (60, 28-77); May (11, 31-61);

July (3, 44-73); Aug. (8, 24-41); Sept. (5, 15-33); Oct. (1, 59); Nov. (21, 35-92); Dec. (11, 40-66).

Gobionellus smaragdus (Valenciennes). Emerald goby*. Station: E(13). Salinity 15.3, temperature 34.1. Number and length: July (1, 57).

Gobiosoma bosc (Lacépède). Naked goby. Stations: A(8, 11, 14, 15), C(3, 16, 24, 28, 31, 35-38), E(12, 22-24, 28, 30-32, 34-37), H(7, 9, 10, 20, 29, 33, 36, 40, 42), I(15). Salinity 0-26.8, temperature 11.0-31.0. Number and length: Jan. (91, 15-40); Feb. (7, 20-37); Mar. (13, 33-50); Apr. (15, 24-42); May (2, 32-38); June (3, 29-34); July (7, 13-41); Aug. (10, 14-26); Sept. (38, 12-32); Oct. (542, 14-47); Nov. (113, 16-33); Dec. (1, 20).

Gobiosoma robustum Ginsberg. Code goby*. Stations: E(14), H(25). Salinity 0-11.0, temperature 14.0-30.0. Number and length: Jan. (4, 20-23); July (1, 26).

Microgobius gulosus (Girard). Clown goby. Stations: C(9, 34, 36-38), E(12, 13, 35-37), F(1), H(4-9, 12, 19, 20, 22, 25, 29, 31, 41, 42), I(1, 4, 6, 7, 9-11, 13, 15, 16, 18, 19, 21), J(3-6, 8), K(1, 4, 5). Salinity 0-19.9, temperature 12.0-34.1. Number and length: Jan. (26, 28-52); Feb. (3, 43-49); Mar. (11, 47-62); Apr. (14, 25-65); May (4, 17-61); June (5, 23-62); July (2, 35-60); Aug. (18, 17-45); Sept. (13, 22-47); Oct. (85, 11-54); Nov. (92, 14-61); Dec. (80, 13-56).

Microgobius thalassinus (Jordan and Gilbert). Green goby*. Stations: A(15, 20, 25), C(13, 15, 24, 36, 37), E(12, 14, 30, 32, 35-37). Salinity 0-26.8, temperature 16.5-30.8. Number and length: Mar. (1, 43); May (2, 46-47); June (4, 23-35); July (12, 24-42); Aug. (1, 32); Sept. (2, 19-21); Oct. (12, 27-42); Nov. (16, 30-36).

Family TRIGLIDAE

Prionotus scitulus Jordan and Gilbert. Leopard searobin*. Station: A(17, 18, 24, 25). Salinity 7.9-24.7, temperature 24.0-28.7. Number and length: June (9, 43-63); Sept. (7, 22-43); Oct. (9, 26-58).

Prionotus tribulus Cuvier. Bighead searobin*. Stations: A(3, 8, 11, 12, 15, 19, 20), C(6, 8, 15, 26, 35, 36, 39), E(19, 21, 32). Salinity 0-26.8, temperature 11.0-29.5. Number and length: Jan. (1, 68); Feb. (5, 61-88); Mar. (8, 19-93); Apr. (2, 28-71); May (2, 38-

67); June (1, 32); July (3, 32-36); Sept. (5, 37-72); Oct. (1, 39); Nov. (2, 46-47).

Family URANOSCOPIDAE

Astroscopus y-graecum (Cuvier). Southern stargazer*. Stations: A(11), D(3). Salinity 11.4-18.3, temperature 11.7-18.5. Number and length: Jan. (1, 65); Mar. (2, 45-55).

Family BLENNIIDAE

Chasmodes bosquianus (Lacépède). Striped blenny*. Stations: A(9), E(13). Salinity 10.8-15.3, temperature 13.0-34.1. Number and length: Feb. (2, 51-63); July (1, 39).

Hypsoblennius hentzi (Lesueur). Feather blenny*. Station: A(11, 17). Salinity 11.4-24.7, temperature 18.5-26.6. Number and length: Mar. (3, 56-66); June (1, 65).

Hypsoblennius ionthas (Jordan and Gilbert). Freckled blenny*. Station: A(17). Salinity 24.7, temperature 26.6. Number and length: June (1, 36).

Undetermined *Hypsoblennius*. Station: A(16, 19, 21, 24-26). Salinity 7.9-23.1, temperature 17.4-29.8. Number and length: May (1, 62); July (1, 53); Aug. (1, 40); Sept. (3, 62-72); Oct. (2, 22-52); Nov. (2, 61-62).

Family OPHIDIIDAE

Ophidion welshi (Nichols and Breder). Crested cusk-eel*. Station: A(2, 5). Salinity 20.8-27.3, temperature 21.5-25.2. Number and length: Mar. (9, 69-179); May (3, 128-145).

Family STROMATEIDAE

Peprilus alepidotus (Linnaeus). Southern harvestfish*. Stations: B(5), D(3). Salinity 16.0-18.3, temperature 11.7-28.3. Number and length: Jan. (2, 81-90); Sept. (1, 96).

Family SPHYRAENIDAE

Sphyraena barracuda (Walbaum). Great barracuda*. Station: A(20). Salinity 14.5, temperature 29.2. Number and length: July (1, 41).

Family MUGILIDAE

Agnonostomus monticola (Bancroft). Mountain mullet. None captured.

Mugil cephalus Linnaeus. Striped mullet. Stations: A(10, 12, 17, 18, 23, 25, 26), B(6), C(13, 18, 26, 29, 32-34), E(22, 24, 28-32, 36), H(17, 20, 29). Salinity 0-25.2, temperature 13.0-31.5. Number and length: Mar. (23, 24-166); Apr. (31, 22-330); June (69, 32-254); July (14, 76-330); Aug. (8, 122-381); Sept. (2, 131-159); Oct. (3, 117-164); Nov. (6, 145-155); Dec. (13, 24-229).

Mugil curema Valenciennes. White mullet. Stations: A(19, 21), B(6), C(15, 16, 21, 31, 33-35), E(19, 22, 28-31, 33-35, 37), H(17, 20), I(17). Salinity 0-22.1, temperature 16.5-31.5. Number and length: Mar. (22, 22-139); June (56, 45-167); July (83, 48-92); Aug. (24, 75-169); Sept. (14, 93-130); Oct. (9, 113-125); Nov. (13, 108-170).

Family ATHERINIDAE

Labidesthes sicculus (Cope). Brook silverside. F

Membras martinica (Valenciennes). Rough silverside. Station: A(25). Salinity 7.9, temperature 26.2. Number and length: Oct. (25, 32-75).

Menidia beryllina (Cope). Tidewater silverside. Stations: A(16-19), C(15, 18, 28, 31, 32, 35-39), E(27, 28, 30, 31, 33), G(3), H(3, 4, 8, 18, 20), I(2, 3, 6, 17), J(2-6, 8), K(3), L(3). Salinity 0-24.7, temperature 12.0-31.6. Number and length: Jan. (1, 45); May (51, 25-42); June (363, 18-53); July (71, 38-57); Aug. (6, 38-56); Sept. (38, 19-52); Oct. (28, 23-42); Nov. (8, 27-49); Dec. (13, 21-54).

Menidia menidia (Linnaeus). Atlantic silverside. Stations: A(10-12, 15, 20-22, 24-26), C(26, 34, 36), E(35, 36). Salinity 0-26.8, temperature 17.4-31.5. Number and length: Mar. (100, 65-96); Apr. (54, 57-96); May (3, 69-79); July (50, 55-65); Aug. (520, 38-59); Sept. (21, 54-63); Oct. (40, 32-71); Nov. (17, 37-72).

Family BOTHIDAE

Ancylopsetta quadrocellata Gill. Ocellated flounder*. Station: A(6, 8, 11). Salinity 7.7-25.8, temperature 11.0-19.3. Number and length: Feb. (4, 55-67); Mar. (1, 85); Apr. (3, 34-59).

Citharichthys spilopterus Günther. Bay whiff. Stations: A(15-17, 19, 20), B(6), C(2, 7-9, 11-15, 25, 27-29, 33-35, 39), E(3, 11-18, 28, 30, 32, 34-37), H(5, 19, 40), I(2). Salinity 0-26.8, temperature 16.5-34.1. Number and length: Apr. (3, 38-86); May (45, 26-93); June, (90, 31-97); July (45, 38-121); Aug. (35, 41-125); Sept. (14, 97-126); Oct. (8, 26-124); Nov. (5, 51-62).

Etropus crossotus Jordan and Gilbert. Fringed flounder*. Stations: A(8, 9, 17, 24-26), B(1, 6), E(14). Salinity 7.7-28.0, temperature 11.0-30.0. Number and length: Feb. (2, 69-72); Mar. (1, 89); June (3, 35-42); July (1, 78); Sept. (4, 33-88); Oct. (6, 28-89); Nov. (1, 56).

Paralichthys albigutta Jordan and Gilbert. Gulf flounder. Stations: A(8, 16, 17), C(6, 16), E(17). Salinity 7.7-24.7, temperature 11.0-30.8. Number and length: Feb. (5, 127-168); Mar. (2, 51-57); May (1, 71); June (3, 66-68); Sept. (1, 139); Nov. (1, 159).

Paralichthys dentatus (Linnaeus). Summer flounder*. Stations: A(15), C(7). Salinity 20.0-26.8, temperature 23.5. Number and length: Apr. (1, 73); May (2, 65-86).

Paralichthys lethostigma Jordan and Gilbert. Southern flounder. Stations: A(9, 21, 22), B(2), C(6, 8, 14, 16, 17, 21, 29, 30, 35, 39), E(10, 12, 18), G(2), H(3, 20, 29, 38), I(2). Salinity 0-30.2, temperature 12.0-31.0. Number and length: Feb. (1, 311); Mar. (19, 22-56); Apr. (6, 40-78); May (6, 67-155); June (43, 61-145); Aug. (3, 257-503); Sept. (6, 106-201); Oct. (1, 139); Nov. (3, 112-202); Dec. (6, 129-144).

Undetermined *Paralichthys*. Stations: A(1, 3, 10-12, 15, 18-20), C(10-13, 21-28, 30-32, 36-38), E(13-15, 22-25, 27, 32, 34), H(4, 19, 25, 30, 32, 33, 37, 41), I(4, 12, 13). Salinity 0-26.8, temperature 14.0-34.1. Number and length: Jan. (1, 210); Mar. (126, 15-254); Apr. (104, 32-178); May (43, 25-362); June (9, 71-240); July (27, 54-231); Aug. (13, 89-356); Sept. (3, 106-191); Oct. (4, 110-164).

Scophthalmus aquosus (Mitchill). Windowpane*. Station: E(19). Salinity 5.5, temperature 19.4. Number and length: Nov. (1, 122).

Family SOLEIDAE

Achirus lineatus (Linnaeus). Lined sole*. Stations: A(15), C(15, 21), E(20). Salinity 0-26.8, temperature 11.0-23.5. Number and length: Mar. (1, 96); May (1, 31); Oct. (1, 77); Dec. (1, 92).

Trinectes maculatus (Bloch and Schneider). Hogchoker. Stations: A(1-5, 8, 11), C(9, 10, 25, 34, 36, 37), D(3), E(1, 2, 13, 14, 22, 35-37), F(1), G(2, 3), H(1, 2, 4-14, 16, 18-22, 25-42), I(1-16, 18-21), J(1-8), K(1-5), L(1-3). Salinity 0-28.2, temperature 8.8-34.1. Number and length: Jan. (116, 26-108); Feb. (90, 27-128); Mar. (785, 16-172); Apr. (230, 25-112); May (170, 36-114); June (220, 15-122); July (140, 16-118); Aug. (189, 17-123); Sept. (70, 15-103); Oct. (366, 17-140); Nov. (240, 28-135); Dec. (231, 25-121).

Family CYNOGLOSSIDAE

Symphurus plagiusa (Linnaeus). Blackcheek tonguefish. Stations: A(1, 8-12, 15-22, 24-26), B(6), C(2, 9-11, 14, 16, 17, 21, 25, 27, 29-39), D(3), E(10, 13-15, 22, 24, 25, 28, 30-32, 34-37). Salinity 0-26.8, temperature 11.0-34.1. Number and length: Jan. (8, 32-81); Feb. (21, 44-106); Mar. (50, 31-88); Apr. (7, 32-115); May (4, 25-77); June (20, 19-81); July (47, 19-68); Aug. (35, 11-76); Sept. (55, 18-92); Oct. (91, 18-84); Nov. (28, 22-152); Dec. (3, 33-37).

Family GOBIESOCIDAE

Gobiesox strumosus Cope. Skilletfish*. Stations: A(8), C(21), E(19). Salinity 0-7.7, temperature 11.0-19.4. Number and length: Feb. (1, 40); Mar. (1, 40); Nov. (1, 38).

Family BALISTIDAE

Stephanolepis hispidus (Linnaeus). Planehead filefish*. Stations: A(15-18), C(27, 29), E(3, 11-14, 26-29). Salinity 11.0-26.8, temperature 22.8-34.1. Number and length: May (12, 17-60); June (14, 21-59); July (3, 65-70).

Family TETRAODONTIDAE

Sphaeroides maculatus (Bloch and Schneider). Northern puffer*. Stations: A(16-19), C(10, 26, 29), E(12, 13, 28, 32, 33). Salinity 6.7-24.7, temperature 23.0-34.1. Number and length: Apr. (1, 16); May (1, 19); June (25, 18-56); July (4, 42-64); Aug. (1, 40).

Family DIODONTIDAE

Chilomycterus schoepfi (Walbaum). Striped burrfish*. Stations: C(15), E(3, 4). Salinity 11.1-14.3, temperature 21.0-30.8. Number and length: June (1, 23); Aug. (1, 101); Oct. (1, 39).

Family BATRACHOIDIDAE

Opsanus tau (Linnaeus). Oyster toadfish. Stations: A(1, 11, 14, 17, 19-21, 24-26), B(6), C(19), E(6, 18, 24, 30, 32, 33). Salinity 0-24.7, temperature 14.0-30.0. Number and length: Jan. (1, 51); Mar. (3, 133-233); Apr. (4, 130-161); June (2, 118-172); July (22, 18-289); Aug. (3, 26-163); Sept. (2, 135-229); Oct. (4, 89-205); Nov. (7, 88-205).

Family OGCOCEPHALIDAE

Ogcocephalus cubifrons (Richardson). Shortnose batfish. None captured.

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Bureau of Commercial Fisheries, Biological Laboratory, Beaufort, N. C. 28516

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THE OARFISH, *REGALECUS GLESNE*: A NEW OCCURRENCE AND PREVIOUS RECORDS FROM THE GULF OF MEXICO.—A large stranded oarfish [*Regalecus glesne* (Ascanius)] was collected at St. Petersburg Beach, Fla., 6 April 1967, by Rear Admiral Edward Ellsberg, U. S. Navy (Ret.). It was identified by Edgar L. Arnold, Jr., Bureau of Commercial Fisheries, St. Petersburg Beach, who notified us. The standard length before preservation was 11 ft, two inches (3404 mm)—the largest oarfish known to us from the Gulf of Mexico. The specimen lacked caudal rays but otherwise was intact except for a vertical wound that partly severed a posterior section of about

Table 1. Records of Oarfish, *Regalecus glesne*, from the Gulf of Mexico.

Date	Locality	Deposition	Authority
20 Mar 1920	Long Key, Manatee Co., Fla.	–	Welsh, 1920
24 Mar 1954	Clearwater Beach, Pinellas Co., Fla.	BCF, St. Petersburg Beach, Fla.	Barnett[1]
June 1954	Clearwater Beach, Pinellas Co., Fla.	Sea-Orama, Clearwater Beach, Fla.	Springer and Woodburn, 1960
26 Feb 1955	90 mi. S. Mobile, Ala. at 29°14′ N. 87°53′ W	USNM 164226	Bullis and Arnold, 1956 Springer and Bullis, 1956
24 Mar 1960	Treasure Island, Pinellas Co., Fla.	–	Hutton, 1961; Springer, 1961
25 Mar 1960	Clearwater Beach, Pinellas Co., Fla.	–	Do.
26 Mar 1960	Indian Rocks Beach, Pinellas Co., Fla.	Univ. Miami Marine Lab.	Do.
26 Mar 1960	Placida, Charlotte Co., Fla.	Cape Haze Marine Lab.	Clark[2]
22 Apr 1962	Englewood, Sarasota Co., Fla.	–	Do.
31 Mar 1963	Longboat Key, Sarasota Co., Fla.	Cape Haze Marine Lab.	Do.
Mar 1964	Clearwater Beach, Pinellas Co., Fla.	–	Do.
1 Apr 1964	Sarasota, Sarasota Co., Fla.	–	Do.
10 Mar 1966	Siesta Key, Sarasota Co., Fla.	Cape Haze Marine Lab.	Earle[3]
12 Mar 1966	Longboat Key, Sarasota Co., Fla.	Manatee Junior College	Keeler[4]
6 Apr 1967	St. Petersburg Beach, Pinellas Co., Fla.	USNM 201458	This paper

[1] Harris Barnett, Sea-Orama, Clearwater Beach., Fla.; [2] Eugenie Clark, Cape Haze Mar. Lab., Sarasota, Fla.; [3] Sylvia A. Earle, Cape Haze Mar. Lab., Sarasota, Fla.; [4] Carl Keeler, Manatee Jr. College, Bradenton, Fla.

two ft (610 mm). It was a male; the stomach was empty. It has been deposited in the U. S. National Museum (No. 201458).

According to Bullis and Arnold (1956), the first published record of *R. glesne* for the Gulf of Mexico was by Welsh (1920) who wrote of a 7-ft (2134 mm) oarfish collected 20 March 1920, at Long Key, Manatee County, Fla. To the best of our knowledge, our specimen brings to 15 the total number of authenticated records for *R. glesne* in the Gulf (Table 1). Except for a single specimen netted at 450 m (Bullis and Arnold, 1956), all have been found stranded or nearly so in spring and early summer along the central west coast of Florida between Placida and Clearwater Beach.

R. glesne is regarded as an oceanic fish of middepths that feeds on small crustaceans (Walters, 1959). Although sharks (Walters, 1959), red tide (Hutton, 1961), storms (Goode and Bean, 1895), and migration for breeding (Serventy, 1966) have been implicated as cause for oarfish strandings none satisfactorily explains the periodic, seasonal occurrence of *R. glesne* on the Gulf beaches of Florida.

This is contribution No. 34, Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fla.

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John L. Taylor and Carl H. Saloman, *Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida 33706.*

Effects of Bottom Substrate on the Brackish Water Bivalve *Rangia cuneata*

KENNETH R. TENORE
Department of Zoology
North Carolina State University
Raleigh, North Carolina 27607

DONALD B. HORTON
Pamlico Marine Laboratory
North Caroline State University
Aurora, North Carolina 27806

THOMAS W. DUKE
Bureau of Commercial Fisheries
Radiobiological Field Station
Gulf Breeze, Florida 32561

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KENNETH R. TENORE
Department of Zoology
North Carolina State University
Raleigh, North Carolina 27607

DONALD B. HORTON
Pamlico Marine Laboratory
North Caroline State University
Aurora, North Carolina 27806

THOMAS W. DUKE
Bureau of Commercial Fisheries
Radiobiological Field Station
Gulf Breeze, Florida 32561

ABSTRACT: The effect of bottom sediment composition on the pelecypod mollusc *Rangia cuneata,* was investigated in the Pamlico River estuary, North Carolina. Mortality meat weight:shell weight ratio, and shell growth were evaluated in relation to particle size, organic matter concentration, and phosphate concentration in the sediment. *In situ* factorial experiments were carried out for 5 months using indivdually marked clams placed in boxes of predetermined sediment composition. Clay-silt sediments were found to be an unfavorable environmental substrate. The detrimental effect was greater in sediments containing high levels of organic matter and phosphate, suggesting that physical and chemical factors associated with finer sediments were responsible. However, in sand sediments, high levels of organic matter and phosphate were found to be favorable to *Rangia*.

To clarify these field results, clams were placed in trays with sediment containing zinc-65 labeled detrital matter and phosphate-32. The results indicated that *Rangia* can accumulate these materials from the sediment. Although *Rangia* is morphologically a typical filter-feeding bivalve, this species appears to obtain organic matter and phosphate from the sediment by direct ingestion or by feeding on bacteria associated with these materials. Such mechanisms are suggested as a possible cause of the better growth observed in sand sediments with moderately high levels of organic matter and phosphate.

Introduction

Rangia cuneata (Gray, 1831) is a pelecypod mollusc of the family Mactridae found in brackish water environments of the southern Atlantic and Gulf coasts of the United States. Its size ranges from 2.5 to 6 cm in length. Abbott (1954) gave the species range as extending from Texas to northwest Florida. Along the coast of the Gulf of Mexico, *Rangia* is often abundant in fresh to brackish water habitats. However, Pfitzenmeyer and Drobeck (1964) reported the occurrence of *Rangia* in the Potomac River, Maryland, and its presence has been reported for other southeastern coastal areas (Chanley, 1965).

The Pamlico River estuary, a continuation of the Tar River, extends from Washington, North Carolina, for about 40 miles to Pamlico Sound. *Rangia* appears to be one of the dominant benthic bivalves in the estuary; its distribution extends from freshwater above Washington, N. C., to the mouth of the Pamlico River (18‰ salinity).

The importance of the effect of bottom sediment type on benthic species has often been emphasized. The work of Peterson (1911, 1913, 1915), describing the bottom communities of Danish waters, is the classical beginning of the study of marine benthic ecology. Thorson (1957) reviewed Peterson's concepts of benthic communities and the work of other ecologists interested in the factors influencing level bottom communities. He emphasized the importance of the relationship between community composition and environmental factors, especially the composition of the bottom substrate. Fairbanks (1963), in a study of the distribution of *Rangia* in Lake Pontchartrain, Louisiana, suggested that the observed differences in population densities were attributable to a difference in substrate types.

Although a great part of the work investigating substrates has involved correlations between the presence or density of different species and different substrate types, little experimental work has been reported concerning the causes of these correlations. This research concerns the causes of observed relationships between bottom substrate and benthic fauna. The influence of substrate type (particle size), organic matter levels, and phosphate levels on *Rangia* was investigated in a field experiment. Various indicators of ecological condition, such as growth, mortality, and meat: shell weight ratios, were used to evaluate substrate effects. To clarify the causes of such influences, the possible utilization of detrital matter and phosphate in the sediments by *Rangia* was investigated in the laboratory utilizing radioisotope tracer techniques.

Field Study of the Effect of Sediment Composition

EXPERIMENTAL PROCEDURE

A field experiment was designed to determine the effect of the composition of bottom sediments on *Rangia*. Three aspects of sediment composition were considered: particle size (clay and sand), organic matter concentration (low level and high level), and phosphate concentration (low level and high level).

Two *in situ* factorial experiments were conducted simultaneously. Complete randomized block designs were used in both factorial experiments, each a 2 (particle size) × 2 (concentration) × 3 (replicate) design. One experiment considered the effect of particle size and organic matter concentration. The other considered the effect of particle size and phosphate concentration. This division was necessary because the organic matter was also high in phosphates.

Sand and clay-silt substrates, which constitute the basic sediment types in the Pamlico River estuary, were the two particle sizes used in the experiment. These substrates were collected in the vicinity of the Pamlico Marine Laboratory on South Creek, a tributary of the Pamlico River. Analysis of particle size composition was determined by standard sieve and hydrometer methods (Day, 1965). A modified Wakely-Black chromic acid oxidation method, employing Ag_2SO_4 to complex the chlorine ions present, was used to determine the organic matter concentration; phosphate concentration was determined by a HCl-H_2SO_4 extraction and colometric procedure (Jackson, 1958). The sand substrate was clean beach sand (particle size averaging 250 to 500 μ), which did not contain any detectable amounts of organic matter or phosphate. The clay-silt substrate (90% of particle size less than 50 μ), collected from shore deposits, contained 0.1% by weight of organic matter and 0.001% by weight of phosphate.

Two levels of organic matter were used: a low level of 0.1% and a high level of 1%. This range of concentrations was chosen to span the low natural level of organic matter found in the clay-silt substrate and the high level reported by Bader (1954), who found high pelecypod densities in association with moderately high levels of organic matter in the sediment. The 1% level approximates such a "beneficial" concentration.

Natural sediment from the estuary, containing 6% of organic matter, was mixed with the sand and clay-silt substrates to obtain the desired organic matter concentrations. Four sediment types were prepared: a sand sediment containing a low level (0.1%) of organic matter; a sand sediment containing a high level (1%) of organic matter; a clay-silt sediment containing a low level (0.1%) of organic matter; and a clay-silt sediment containing a high level (1%) of organic matter.

In the experiment investigating the effect of phosphate concentration, two levels of phosphate were used: a low level of 0.001% and a high level of 0.1%. The low level was determined by the natural level of phosphate in the clay-silt sediment. High grade phosphate ore, $Ca_{20}FCO_3(PO_4)$, insoluble in water and containing 33% phosphate measured as P_2O_5, was obtained from the Texas Gulf Sulfur Phosphate mine near Aurora, North Carolina. This ore material was used in view of the possibility of phosphate enrichment of the Pamlico River estuary from mining activities. This material was added to the sand and clay-silt substrates to obtain the 0.001% and 0.1% concentration levels. Four sediment types were prepared: a sand sediment containing a low level (0.001%) of phosphate; a sand sediment containing a high level (0.1%) of phosphate; a clay-silt sediment containing a low level (0.001%) of phosphate; a clay-silt sediment containing a high level (0.1%) of phosphate.

Three boxes (0.9 m × 0.6 m × 0.4 m) of each of the eight sediment types were prepared and randomly positioned offshore in South Creek in an area of uniform environment. The boxes were spaced 2 m apart to avoid any interactions of sediment exchange processes. *Rangia* were collected in the vicinity of the Pamlico Marine Laboratory. The linear size (maximum anterior-posterior length) of the clams was measured with calipers; each clam was numbered and its size recorded; and 14 clams were placed in each of the boxes. The boxes were left undisturbed from June to November, 1966. The clams were collected at the end of this time period, the mortality in each box was recorded, and the final linear size, the meat weight, and the shell weight of each clam was determined.

TABLE 1. Treatment means for percentage mortality of *Rangia cuneata* and *lsd* values[1] for treatment comparisons. The means are based on three replicates.

Sediment type	Organic matter concentration		Main effect
	0.1%	1%	Sediment type means
Clay-silt	26.20	40.63	33.40
Sand	11.87	4.70	8.29

lsd for sediment type main effect means.... 9.89
lsd for sediment type-organic matter combinations.............................. 13.40

Sediment type	Phosphate concentration		Main effect
	0.001%	0.1%	Sediment type means
Clay-silt	23.80	57.17	40.49
Sand	21.46	21.43	21.44

lsd for sediment type main effect means.... 16.67
lsd for sediment type-phosphate combinations.............................. 23.60

[1] All *lsd* (least significant difference) values are at 0.05 probability level and based on 8 df for variance estimates.

RESULTS AND DISCUSSION

MORTALITY

The percentage loss of clams in each box over the five-month period was used as a measure of mortality. Arcsin transformation of data was used and an analysis of variance and least significant difference (*lsd*) comparsion at .05 probability level of these data (Table 1) indicated:

1. Clams in the clay-silt sediments showed significantly higher mortality than those in the sand sediments.
2. Clams grown in the clay-silt sediment with the high level of phosphate showed significantly higher mortality than those in the low level of phosphate.
3. Clams grown in the clay-silt sediment

with the high level of organic matter showed significantly higher mortality than those in the low level of organic matter.

Many factors could be responsible for the significantly higher mortality in the clay-silt sediments. The clams in this sediment type did not burrow as deeply as those in the sand sediments and could have been more susceptible to predation by crabs. This observed difference in burrowing could be due to the physical difficulty in burrowing in a more compact sediment or to a response by the clams to physicochemical properties of the clay-silt sediments. Pratt (1953) observed a difference in the vertical distribution of *Mercenaria* in different sediment types. Clams were found nearer the surface in fine sediments. He associated this with the low water permeability of fine sediments that results in depletion of oxygen and accumulation of decomposition products. The higher mortalities in the clay-silt sediments containing high organic matter and high phosphate concentrations may have been due to an intensification of these factors.

MEAT WEIGHT: SHELL WEIGHT RATIO

Allometric relationships of one body part to another have been shown to vary in bivalves due to a variety of environmental factors (Wilbur and Owen, 1964; Allen, 1963). The ratio of meat weight to shell weight is a useful allometric relationship used as a "condition" index in studying environmental effects on bivalves. A high value of this ratio indicates more favorable environmental conditions; a low value suggests more adverse conditions (Allen, 1963). Butler (1952) states that this measurement is not valid if observations are made over different periods of time since meat condition changes with season and spawning condition, but the measurement may be used to compare responses to environmental factors in a particular experiment.

The condition index was calculated for each clam. An analysis of variance and least significant difference (*lsd*) comparison of treatment means (Table 2) indicated:

1. Clams grown in the sand sediments showed significantly higher ratios than those grown in the clay-silt sediments.
2. Clams grown in the clay-silt sediments showed significantly higher ratios at low organic matter levels than those grown in the high organic matter level.

These results show that the clams were adversely affected by the clay-silt sediment environment. In this sediment type, the higher ratios for clams maintained in low organic matter concentrations compared to clams in high organic matter concentrations indicates that higher concentrations of organic matter intensifies this adverse effect.

SHELL GROWTH

Linear measurements, e.g. linear shell increments, are commonly employed as an indicator of growth responses of molluscs to environmental conditions. Measurement of a body part is assumed to be proportional to the growth of the whole organism over most of its life history and thereby provides a general index for measuring growth.

TABLE 2. Treatment means for meat weight: shell weight ratio of *Rangia cuneata* and *lsd* values[1] for treatment comparisons. The means are based on three replicates.

Sediment type	Organic matter concentration		Main effect
	0.1%	1%	Sediment type means
Clay-silt	0.188	0.146	0.167
Sand	0.195	0.205	0.200

lsd for sediment type main effect means... 0.153
lsd for sediment type-organic matter combinations.............................. 0.0216

Sediment type	Phosphate concentration		Main effect
	0.001%	0.1%	Sediment type means
Clay-silt	0.173	0.169	0.171
Sand	0.186	0.193	0.189

lsd for sediment type main effect means.. 0.0079
lsd for sediment type-phosphate combinations.............................. 0.0112

[1] All *lsd* (least significant difference) values are at 0.05 probability level and based on 8 df for variance estimates.

A comparison using the mean increment value from each box was used as a relative measure of shell growth. Analysis of variance and least significant difference (*lsd*) comparison of the treatment means (Table 3) indicated:

1. Clams grown in the sand sediments showed greater growth than clams grown in the clay-silt sediments.
2. Clams grown in sand with the high concentration of organic matter showed greater growth than clams grown in the low concentration of organic matter.

Since an increase in shell size is a general index of the growth of the whole organism, shell growth is affected not only by general environmental conditions, but also specifically by the availability of food material to the clam. The results indicated that there was a greater growth among clams in the sand sediments containing the high level of organic matter than those in the low level of organic matter. This difference might reflect a greater supply of food available to the clams in the sand sediments with the high level of organic matter.

TABLE 3. Treatment means for shell growth of *Rangia cuneata* and *lsd* values[1] for treatment comparisons. The means are based on three replicates. Shell growth is in mm.

Sediment type	Organic matter concentration		Main effect
	0.1%	1%	Sediment type means
Clay-silt	0.37	0.28	0.33
Sand	0.44	0.62	0.53

lsd for sediment type main effect means 0.028
lsd for sediment type-organic matter combinations 0.040

Sediment type	Phosphate concentration		Main effect
	0.001%	0.1%	Sediment type means
Clay-silt	0.39	0.28	0.34
Sand	0.43	0.50	0.47

lsd for sediment type main effect means 0.105
lsd for sediment type-phosphate combinations. 0.149

[1] All *lsd* (least significant difference) values are at 0.05 probability level and are based on 8 df for variance estimates.

The combined results derived from observing the three indices of mortality, meat-shell ratio, and shell growth may be summarized as follows:

1. All three indices indicate that sand is a more favorable environmental substrate than clay-silt.
2. Mortality and meat: shell ratio data indicate that high phosphate and organic matter concentrations in clay-silt sediments have an adverse effect on *Rangia*.
3. There was significantly greater growth in the clams maintained in sand sediment containing the high level of organic matter than in those in the sand with the low level of organic matter. Greater growth was also found in the clams maintained in sand with the high level of phosphate than in those in the sand with the low level of phosphate, but this was not statistically significant.

Regarding the effect of organic matter and phosphate concentrations in the sediments, no one particular index measurement indicated all of the results summarized above. This could be due to problems associated with the experimental design. The duration of the experiment (5 months) may be too short to expect large changes in growth and allometric relationships. This is especially so since relatively large clams were used. Juvenile clams could be expected to have a more sensitive response to environmental influences. Also, a change in the initial organic matter and phosphate levels could be expected due to the influence of the current, turbidity, and silt deposition found in the estuarine environment.

An important aspect of this experiment is that the boxes were all placed in a uniform environment in the estuary. Many investigators (Pratt and Campbell, 1956; Sanders, 1958) have suggested that one of the main causes of the observed relationships between benthic organisms and sediments are those factors associated with overlying water masses, such as current velocity, turbidity, and planktonic food source. Since in this experiment these environmental influences were presumably uniform, the results can be attributed to the sediment composition factors.

The fact that growth was greatest in

clams maintained in sand sediment with the high levels of organic matter or phosphate suggests that these sediment materials may be used as a food material by *Rangia*. According to Davis (1925), the association of benthic fauna with sediments of a particular nature or texture is not so much influenced by particle size *per se* as by the differing food sources found in various sediment types. This important ecological concept concerning the sediment as a food source for benthic communities was formulated by the early Danish investigators, Peterson (1911), Blegvad (1914), and Jensen (1919). Ekman (1947), correlating the presence and abundance of individual species and groupings or communities of benthic forms with substrate types, also emphasized the importance of the role of detrital matter in the sediments as a primary source of food for bottom species. Bader (1954) states that although the other physical variables are by no means unimportant, the organic content of the sediments and its state of decomposition apparently controls pelecypod densities. He found an increase in the densities of pelecypod populations with a moderate increase of the organic matter concentration of the sediments. However, with higher organic matter concentrations there was an increase of decomposition products due to bacterial action. Under such conditions, pelecypod densities were low. He suggested that the unoxidized or undecomposed detrital matter may serve as a food source and that this is depleted by bacterial decomposition. Fairbanks (1963) suggested that higher organic matter concentrations were a factor responsible for greater population densities in Lake Pontchartrain.

Phosphate is another component of the bottom sediments that has been investigated as an environmental factor affecting animal-sediment relations. The ability of lamellibranchs to obtain phosphates directly from sea water has been demonstrated by Ronkin (1950) and Pomeroy and Haskin (1954). Bivalves might utilize phosphates directly from the sediments, for Cooper (1948) found bivalves to thrive best in sediments with higher phosphate (inorganic) content.

Accumulation of Detritus and Phosphate from the Sediment

Our field study indicates that both organic matter and phosphate concentrations in the sediment affect the physiological condition of *Rangia*. One of the causes of this observed sediment-animal relation might be the capacity of *Rangia* to use these components of the sediment as a nutrient source. Experiments using radioisotope tracer techniques were carried out to investigate this hypothesis.

The use of isotopes in studying the feeding activities of animals has certain advantages. The utilization and assimilation of labeled food material can be measured directly by determining the presence of the label isotope in the animal tissue. In comparison with such indirect indices as growth and mortality, isotope tracer methods are more sensitive, accurate, and efficient in studying the utilization of different food sources.

Zinc occurs naturally in plants and animals, being involved in enzymatic systems in respiration processes (Vallee, 1959). Algae are easily labeled with zinc-65, and the uptake and exchange processes are more stable than other radionuclides (Gutknecht, 1963). Therefore, zinc-65 was used to label detrital matter in this experiment.

A problem associated with the use of radioisotopes to label food materials that are released into an aqueous environment is that the radionuclide may be leached from the food material into the water. It is then difficult to determine whether the animals have accumulated the isotope by ingestion of the labeled food or directly from the water by adsorption to exposed surfaces. This difficulty must be considered in designing an experiment and interpreting the results.

ACCUMULATION OF DETRITAL MATTER

EXPERIMENTAL PROCEDURES

Detrital matter was prepared from zinc-65 labeled algae and then was mixed with a sediment and placed in a flowing sea water system. Clams were placed in the sediment and analyzed periodically for zinc-65 content. The presence of zinc-65 in the animals was presumed to indicate detrital matter utilization.

To prepare the labeled detrital matter, a 6-liter culture of *Chlamydomonas* was inoculated with 333 μc of zinc-65 from a stock solution of carrier-free zinc-65 in 0.5 N HCL. The culture was placed on a magnetic stirrer and incubated under light for 2 days to allow zinc-65 uptake by the algal cells. After this period the culture was centrifuged and the algal material washed by suspending it in fresh sea water. The suspension was then centrifuged and the algal material removed and placed in a water bath at 65 to 75 C for 1 hour to kill the algae without rupturing and disintegrating the cells. Similarly, 111 μc of zinc-65 were added to a Bentonite clay slurry (90% Montmorillinite) and allowed to stand for 24 hours so that the isotope would be sorbed onto the clay surfaces.

A series of four trays (28 cm × 35 cm × 15 cm) containing 8 cm of sand were each connected by plastic tubing to a similar tray below so that the water from each experimental tray drained into a corresponding control tray. The labeled detrital matter was divided among the first three experimental trays and mixed into the middle stratum of the sand substrate. Labeled clay was added to the fourth tray in the same way in an amount to give equal zinc-65 concentrations in all the top trays. In each of these trays, ten clams were placed in the sediment. Five clams were suspended in two of the trays containing the labeled detrital matter and in their connected trays. An average flow rate of 15 liters per hour was maintained during the experiment. Water for the experiment was pumped directly from the end of the pier of the Pamlico Marine Laboratory on South Creek. The experiment was carried out for 5 days in October 1966. The salinity and temperature varied with the South Creek environment, with an average temperature of 18 C and an average salinity of 12‰.

During the experiment, 3-ml water samples were taken from each tray at one-day intervals for determination of the zinc-65 levels in the water. At the termination of the experiment, each whole clam was analyzed for zinc-65 content. Adductor muscle tissues were then dissected, washed in distilled water, and also analyzed. In one tray of each of the treatments, gut material from the clams also was collected for analysis. Determinations of the zinc-65 content were made with a well type scintillation detector connected to a conventional scaler. None of the isotope concentration values were corrected for the relatively slight physical decay (half-life of zinc-65 is 245 days).

A preliminary study using this procedure described above showed that a portion of the zinc-65 in the labeled detrital matter was released into the water. Initially, a large portion of the zinc-65 in the water was in particulate form, but this declined in a few days. The high values observed initially were probably due to the temporary suspension of fine particles of labeled detritus. Since zinc-65 material leached into the water could be expected to interfere with the detection of detrital matter, the several "controls" described above were used to measure the uptake of the leached zinc-65. The continuous flowing water system was used to remove leached zinc-65 from the system, reducing the amount of zinc-65 available to the clams from the water. Clams in the trays containing unlabeled sand and receiving the water from the experimental trays would presumably be exposed only to the zinc-65 materials present in the water. Clams suspended above the sediment in the experimental trays assured a more accurate measure of the zinc-65 uptake from the water since the accumulation of zinc-65 by the sediment in the control trays might reduce the magnitude of the zinc-65 uptake by the clams in the control trays. Clams maintained in the tray containing zinc-65 labeled clay determined the contribution of leached zinc-65 contained in the sediment and interstitial water to the total zinc-65 accumulation of the experimental clams.

RESULTS AND DISCUSSION

All the whole clams contained significant levels of radioactivity. A *t*-test (at .01 probability level) was used to determine

TABLE 4. A comparison of the zinc-65 content of whole *Rangia cuneata* under different treatments.

Treatment[1]	Zinc-65 content[2]	Treatment	Zinc-65 content	Students "*t*" value
E1	77 ± 57 (10)	C1	7 ± 1 (10)	3.78**
E2	91 ± 29 (10)	C2	6 ± 2 (10)	8.64**
E3	84 ± 39 (10)	C3	11 ± 2 (10)	5.57**
C2	6 ± 2 (10)	E2W	26 ± 3 (5)	16.00**
C3	11 ± 2 (10)	E3W	24 ± 1 (5)	9.66**
E2	91 ± 29 (10)	E2W	26 ± 3 (5)	6.11**
E3	84 ± 39 (10)	E3W	24 ± 1 (5)	3.47**
E1, 2, 3	84 ± 30 (30)	SE	55 ± 21 (10)	1.06

[1] Symbols: E1, E2, E3 represent clams maintained in trays containing labeled detrital matter mixed with sand. C1, C2, C3 represent clams maintained in trays containing sand without labeled detrital matter and receiving water supply from E1, E2, and E3 respectively. E2W, E3W represent clams suspended above the sediment in trays E2 and E3 respectively. SE represents clams maintained in tray containing zinc-65 labeled clay mixed with sand.

[2] Zinc-65 content values given as the mean count/min per gram body wet weight ± 1 standard deviation; number of clams in parentheses.

** Significant at the .01 probability level.

significant differences between the mean zinc-65 content of clams under the various treatments (Table 4). The analysis indicated:

1. There were higher levels of zinc-65 in clams maintained in the trays containing labeled detrital matter than in those in the control trays without detrital matter or in those suspended above the sediment.

2. There were higher levels of zinc-65 in clams suspended above the sediment in the experimental trays than in those maintained in the control trays without labeled detrital matter.

3. There were no significant differences between the zinc-65 content of whole clams maintained in the trays containing the labeled detrital matter and those in the trays containing the zinc-65 labeled clay.

As noted, there were significantly higher zinc-65 concentrations in the whole clams maintained in the trays containing the labeled detrital matter than in those in the unlabeled sand. This difference, however, might be due to the accumulation of zinc-65 leached from the detrital matter into the sediment and water, or to the presence of unassimilated labeled particles at the time of analysis for zinc-65 content. The higher levels of zinc-65 in the clams suspended in the experimental trays compared with those maintained in the unlabeled sand could be due to slightly higher levels of zinc-65 found in the water of the experimental trays than in the control trays. Also because of the "competition" in the accumulation of the isotope from the water by the sediment in the control trays, less zinc-65 was available to the clams in these trays.

However, any change in the normal environment of an organism, such as suspending clams in water, can disrupt and alter the organism's normal functioning. This is one of the problems involved in research investigating aspects of the physiological processes and ecology of benthic forms. Often in such research the animal is removed from its natural environment and placed in an artificial one, *e.g.*, culture dishes. With regard to infaunal benthic forms, there is an intimate relation between the whole ecology of such a species and the substrate within which it lives. Thus, the zinc-65 concentrations in the suspended clams might somehow be due to the separation of the clams from their substrate.

The whole clams from the trays containing labeled detrital matter and labeled clay accumulated more zinc-65 than the clams in the unlabeled substrate or the suspended clams. However, there was no significant difference in the zinc-65 content of the clams maintained in the trays containing labeled detrital matter and labeled clay. Zinc-65 could have been accumulated through processes other than ingestion and assimilation of the labeled detritus, such as accumulation of leached zinc-65 present in the sediment. Therefore, gut material and adductor muscle tissues were analyzed for zinc-65 content. This procedure was used by Floyd (1952) in studying the feeding of oysters with phosphorus-32 labeled algae. His results showed that the presence of the isotope in the muscle tissue was a direct result of the ingestion and assimilation of the labeled algae and not the result of surface adsorption of the isotope from the water medium.

A *t*-test (at .01 probability level) of the zinc-65 content of gut material from clams in one of the trays containing labeled detrital matter, the connected control tray, and the tray containing zinc-65 labeled clay showed that there were significantly higher isotope concentrations in the gut material from the clams maintained in the tray with labeled detrital matter than materials from both the control tray and the tray containing labeled clay (Table 5). Presumably, this higher isotope level is due to the ingestion of labeled detrital matter.

TABLE 5. A comparison of the zinc-65 content of gut material collected from *Rangia cuneata* under different treatments.

Treatment[1]	Zinc-65 content[2]	Treatment	Zinc-65 content	Students "*t*" value
E1	109 ± 45(10)	C1	10 ± 12(10)	3.81**
E1	109 ± 45(10)	SE	3 ± 6(10)	7.11**

[1] Symbols: E1 represents clams maintained in tray containing labeled detrital matter mixed with sand. C1 represents clams maintained in tray containing sand without labeled detrital matter and receiving water supply from E1. SE represents clams maintained in tray containing zinc-65 labeled clay mixed with sand.

[2] Zinc-65 content values given as the mean count/min per 0.5 g ± 1 standard deviation; number of clams given in parenthesis.

** Significant at the .01 probability level.

There were significantly higher levels of zinc-65 in the adductor muscle of clams maintained in the trays with the labeled detrital matter than in the muscle tissue of clams in all the other treatments (Table 6). Assuming that the presence of zinc-65 in the muscle tissue is an index of the incorporation of the labeled food material, the results indicate that the clams ingested and assimilated the zinc-65 from the labeled detritus either directly through ingestion of the detritus, or indirectly through accumulation of zinc-65 from the water, or by both mechanisms. Price (1962) reported the uptake of zinc-65 by molluscs, and this might explain the observed zinc-65 concentrations in the experiment. However, because of the low amounts of zinc-65 in clams maintained in the control trays, the zinc-65 in the muscle tissue of clams maintained in the trays containing labeled detrital matter was probably obtained directly from the ingestion and assimilation of the labeled detrital matter.

ACCUMULATION OF PHOSPHORUS-32

EXPERIMENTAL PROCEDURE

A similar experiment was carried out to investigate the accumulation of phosphate from the sediment by *Rangia*. A stock solu-

TABLE 6. A comparison of the zinc-65 content of adductor muscle tissue of *Rangia cuneata* under different treatments.

Treatment[1]	Zinc-65 content[2]	Treatment	Zinc-65 content	Students "*t*" value
E1	56 ± 27 (10)	C1	1 ± 0.02 (10)	6.44**
E2	132 ± 39 (10)	C2	9 ± 15 (10)	9.14**
E3	146 ± 66 (10)	C3	9 ± 8 (10)	6.19**
E2	132 ± 39 (10)	E2W	6 ± 8 (5)	9.54**
E3	146 ± 66 (10)	E3W	4 ± 7 (5)	6.92**
E1, 2, 3	111 ±.46 (30)	SE	7 ± 10 (10)	11.46**

[1] Symbols: E1, E2, E3 represent clams maintained in trays containing labeled detrital matter mixed with sand. C1, C2, C3 represent clams maintained in trays containing sand without labeled detrital matter and receiving water supply from E1, E2, E3 respectively. E2W, E3W represent clams suspended above the sediment in trays E2 and E3 respectively. SE represents clams maintained in tray containing zinc-65 labeled clay mixed with sand.

[2] Zinc-65 content values given as the mean count/min per gram wet weight ± 1 standard deviation; number of clams in parentheses.

** Significant at the .01 probability level.

TABLE 7. A comparison of the phosphate-32 content of adductor muscle tissue of *Rangia cuneata* under different treatments.

Treatment[1]	Phosphate-32 content[2]	Students "*t*" value	Treatment	Phosphate-32 content
E1	135,525 ± 90,100 (10)	4.6**	C1	3,650 ± 2,410 (10)
E2	152,104 ± 58,100 (10)	8.1**	C2	2,092 ± 1,850 (10)
E2	152,104 ± 58,100 (10)	7.1**	E2W	8,644 ± 3,126 (5)

[1] Symbols: E1 and E2 represent clams maintained in trays containing phosphate-32 mixed with sand. C1 and C2 represent clams maintained in trays containing sand without phosphate-32 and receiving water supply from E1 and E2 respectively. E2W represent clams suspended above the sediment in tray E2.

[2] Phosphate-32 content values given as the mean count/min per g wet weight ± 1 standard deviation; number of clams in parentheses.

** Significant at the .01 probability level.

tion of carrier-free phosphorus-32 (phosphate ion in HCL) was used as a label. Two experimental trays, each containing 30 μc of phosphorus-32 sorbed onto the sediment particles, were connected as described previously to control trays containing unlabeled sand. The water was allowed to flow for 4 hours, then ten clams were added to each tray and five clams were suspended above the sediment in one of the experimental trays.

At daily intervals, 2-ml water samples were collected from each tray. Each water sample was placed on a planchet, evaporated to dryness, and measured for phosphorus-32 concentration. At the end of five days, the adductor muscle tissue from each clam was removed, washed with distilled water, and dissolved in 4 ml of concentrated nitric acid. Each solution then was placed on a planchet, evaporated to dryness, and measured for phosphorus-32 concentration. The isotope measurements used a thin-window proportional counter, and there was no correction for decay.

RESULTS AND DISCUSSION

The isotope levels in the water of the paired trays were similar although the water in the trays containing the phosphorus-32 in the sediment had a higher concentration. The high levels observed could be due to the mixing activity of the flowing water. A *t*-test (0.01 probability level) indicated significantly higher phosphorus-32 levels in the adductor muscle of the clams maintained in the sediment containing phosphorus-32 than in those maintained in the unlabeled sediment and in those suspended above the sediment (Table 7). *Rangia* has the capacity to accumulate phosphorus from the sediment.

Summary and Conclusions

The results of the field study investigating the effect of particle size, organic matter, and phosphate concentrations of bottom sediments on *Rangia cuneata* indicated that clay-silt sediments were more unfavorable as an environmental substrate than were sand sediments. Possible causes of this adverse effect were not investigated. However, the physical nature of a compact, fine sediment and the physico-chemical environment associated with it is thought to have a detrimental effect on infaunal benthic forms. High concentrations of organic matter and phosphate in clay-silt sediments further increased this adverse effect. Perhaps the presence of these materials results in the formation of a reduced, oxygen-depleted environmental substrate.

However, the high concentrations of organic matter and phosphate in sand sediments had a favorable effect on the growth of *Rangia,* probably through an increase in the availability of food material. Past workers have stressed the importance of plankton as a food source for filter-feeding bivalves. The accumulation of zinc-65 labeled detrital matter and phosphorus-32 from the sediment by *Rangia* indicated that this clam, although morphologically a typical filter-feeding bivalve, has the capacity to utilize organic matter and phosphate from the sediment. This utilization might be by direct ingestion and assimilation of these materials, or indirectly by ingestion of bacteria and benthic algae associated with these materials. Therefore, moderately high levels of these materials, resulting in an increase of food material available to bivalves, should be considered as a factor in the understanding of benthic-sediment relationships.

Further work is needed to investigate the degree of importance to *Rangia,* and other infaunal bivalves, of such materials found in the sediment as possible causes of animal-sediment relationships.

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3

Filtration performance

D. J. Tranter
Division of Fisheries and Oceanography
CSIRO
Cronulla, Sydney, Australia

P. E. Smith
Bureau of Commercial Fisheries
La Jolla, California, U.S.A.

SUMMARY

Towing a plankton net through the water disturbs both the water and the plankton it contains. The main disturbances are immediately upstream of the gauze, immediately upstream of the entrance, and in the wake of towing bridles and other obstructions. This interaction between net and water, which determines the volume of water filtered by the net and influences the composition and condition of the catch, constitutes what may be called filtration performance. Its main physical components are filtration efficiency, filtration pressure (pressure drop across the meshes), and perhaps mesh velocity. These change to some extent as the organisms filtered from the water accumulate upon the filtering surface, so adding to the complexity of the filtration process. The laws of fluid mechanics throw some light on this complexity.

The initial filtration efficiency of simple unencased nets made from modern gauze is usually high (> 85 per cent). Towing velocity has little effect upon filtration efficiency above about 1 knot; more information is required about efficiency at lower speeds since, in the future, these may be adopted to minimize damage to the catch. The principal parameters of filtration efficiency in *unencased* nets are the porosity of the gauze and its surface area in relation to the mouth area of the net. Filtration efficiency increases with the area of gauze, reaching a comparative plateau when the open area of the gauze is more than three times the area of the net mouth.

Much less is known about *encased* samplers, because here the filtration efficiency is determined principally by the shape of the sampler rather than by the resistance of the net. Mouth-reducing cones (flares) lead to an increase, and net casings to a decrease, in filtration efficiency. It is possible and perhaps desirable to adjust the initial filtration efficiency to exactly 100 per cent; however, this value would decline with clogging.

Nets made from fine gauze are much more likely to clog than those made from coarse gauze. The volume which may be filtered efficiently before clogging reduces the usefulness of further sampling is increased approximately sixfold by doubling the area of gauze in the net. The rate of clogging can be further reduced by having a porous cylindrical collar in front of the filtering cone; the collar oscillates, probably in response to eddies shed by the ring, and so cleans itself of accumulated organisms. Clogging can be monitored by using two flowmeters, one inside and one outside

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the net, both of which should be clear of local accelerations. A limit can be placed upon the extent of clogging by limiting the distance towed. Further investigations are needed to ease the clogging problem, particularly in encased samplers.

The flow through a plankton net approaches and leaves the gauze at a reduced velocity, accelerating momentarily in transit through the meshes. Damage to the organisms caught would appear to be caused by the pressure drop across the meshes which varies as the square of the approach velocity. Consequently the condition of the catch could probably be improved by lowering the speed of tow, by reducing the mouth area of the net, or by increasing the area of gauze. Mouth-reducing cones will not reduce flow through the net in proportion to the mouth reduction unless the gauze is separated from the faster flow around the net by a non-porous casing. More information is required concerning the effects of filtration pressure upon the plankton organisms in the net.

Acceleration fronts arising from the resistance of the net to the flow through the meshes could warn organisms of the net's approach. Such disturbances extend only a short distance ahead of the net mouth and are strongest at the periphery. Towing a net from the standard triple-leg bridle creates further disturbances ahead of the net; in such cases the flowmeter should not be located in the centre of the net mouth but between the centre and the rim. More attention could be given in design to alternative towing arrangements.

INTRODUCTION

Ever since Hensen initiated quantitative plankton sampling in the late 1800's there has been a gradual shift in emphasis from systematics, diversity, and zoogeography towards plankton ecology. In ecological work, an estimate of the volume of water filtered by the net is usually required, and the statistical treatment of the data obtained depends upon assumptions concerning the filtration performance of the net. It is the purpose of this chapter to review not only the physical basis of filtration in plankton nets but also the practical problems of filtration at sea, so that the design and use of plankton nets can conform to the requirements of a given investigation.

Hensen (1895) developed a method for calculating the volume of water filtered, by means of *filtrationkoefficienten* based on laboratory experiments; Birge (1895) compared catches taken by a net with those taken by a plankton trap from a known volume of water; and Reighard (1897) compared net catches of inanimate particles with their known concentration in the water. Hensen's technique is subject to error due to clogging of the gauze (Kofoid, 1897*b*; Kokubo and Tamura, 1931), particularly with fine nets; this led Reighard (1897) to recommend the use of a flowmeter to measure directly the volume of water filtered during the tow. Flowmeters are now widely adopted for quantitative sampling (Nansen, 1915; Clarke and Bumpus, 1950; Nakai, 1954), and methods for calibrating and using them are described (Harvey, 1934; Nishizawa and Anraku, 1956; Yentsch and Duxbury, 1956; Motoda, Anraku and Minoda, 1957; Ito and Nishimura, 1958; Nakai, 1954; Tranter, 1965; Jossi, 1966; Gehringer and Aron, this volume, Chapter 6).

Other research has attempted to evaluate the 'catching power' of a net. Hensen (1895) and Bridger (1958), for example, found that the use of mouth-reducing cones gave what appeared to be a better catch. Such results have usually proved to be equivocal. To eliminate interference from other sampling effects, recent evaluations of filtration in plankton nets have made use of hydrodynamic test channels (Enomoto, 1955; Sysoev, 1956; Nishizawa and Anraku, 1956; Miller, 1961; Currie, 1963; Higo, 1964; Tranter and Heron, 1965, 1967; Smith and Clutter, 1965; Mahnken and Jossi, 1967) and also wind-tunnels (Tranter and Heron, 1967). The data so derived have helped to evaluate the extent of net clogging at sea (Ito and Nishimura, 1958; Asaoka and Ohwada, 1960) and the rate at which it occurs (Smith, Counts, and Clutter*[1]; Fraser, 1966).

The technical problems of filtration performance are now more tractable than other major quantitative plankton sampling problems, such as patchiness, avoidance and mesh selection.

THEORETICAL BASIS

The planktologist has relied heavily in the past upon the empirical rather than the theoretical approach to filtration in plankton nets, and has met with some degree of success. However, as with most empirical approaches, the power to extrapolate has been severely limited, particularly in view of the diversity of samplers and sampling methods in common use.

The physical properties associated with filtration that are of greatest concern in plankton sampling are *filtration efficiency*, *filtration pressure*, *mesh velocity*, and *drag* (see Terminology). Filtration efficiency directly influences the volume of water filtered, and could also influence avoidance (see Chapter 4) and escapement (see Chapter 5). Filtration pressure influences the ultimate condition of the catch and might influence escapement also. Very little is known about the local acceleration of water through the meshes, but this could have an effect upon escapement distinct from that of filtration pressure. The drag on the net is an important consideration in the field (see Chapter 6) since it influences wire angle and can limit the speed and depth at which a net is towed.

Apart from Hensen's pioneering experiments, few investigations have been made, until recently, on the physical basis of filtration in plankton nets. Hensen (1895) tested the rate of flow of water through 12 silk gauzes at 75 increments of pressure. His experimental technique would appear to be at fault (Fig. 1) in that the flow discharged into still water, so giving an artificially high pressure head on the upstream side (Borda-Carnot effect). Sysoev (1956) measured the resstance of plankton nets in a laboratory flume. The significance of his results might not extend to field conditions because the entire flow through the flume was channelled into the net, and, as Tranter and Heron (1965, 1967) have shown, filtration is influenced in practice by the flow of water round a net.

Despite this, the work of Hensen and Sysoev has thrown a great deal of light upon the physical processes involved in filtration, and these may be further clarified

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[1] Asterisked (*) references denote information presented at the Sydney Symposium.

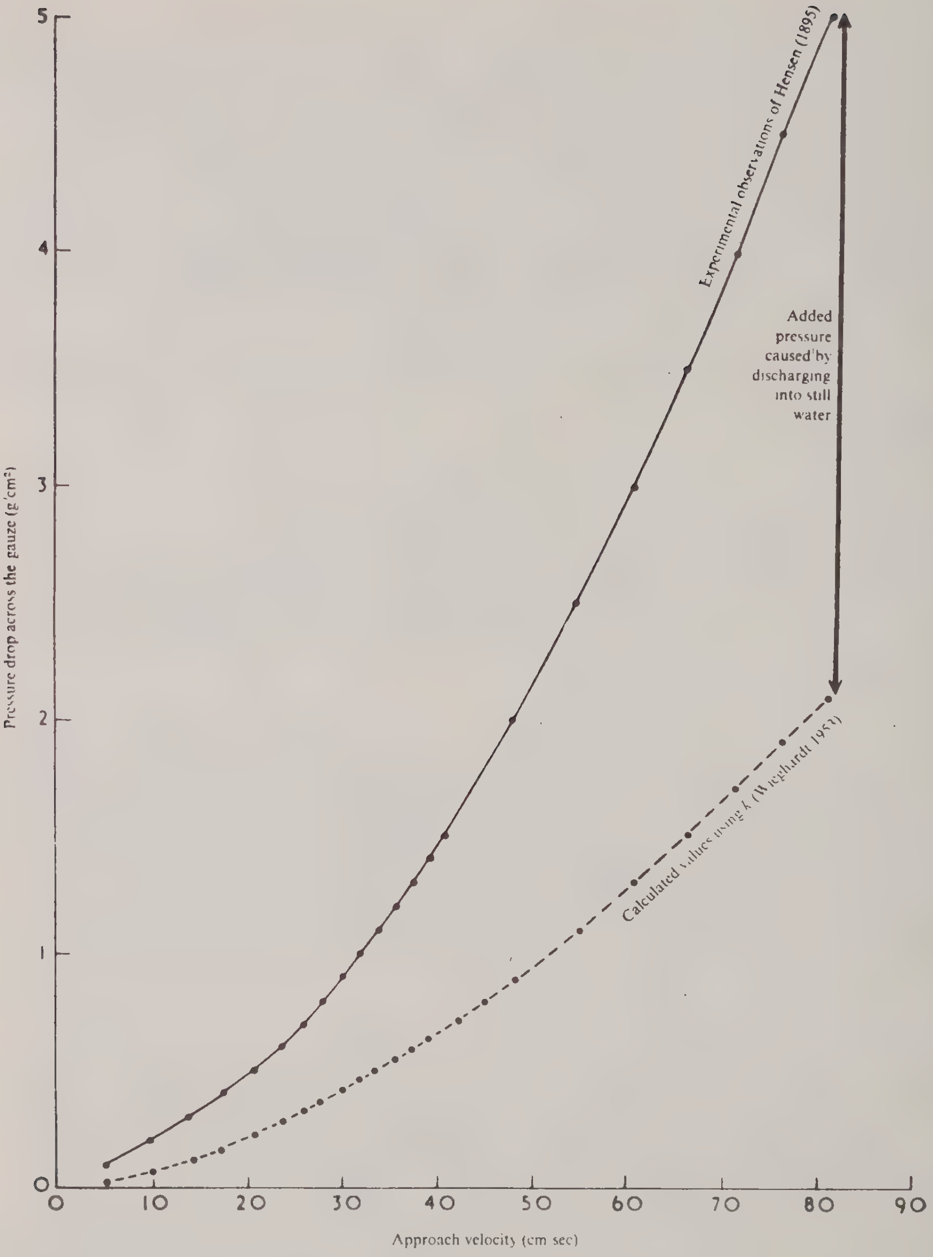

Figure 1
Relation between the velocity of a stream of water normal to a gauze and the pressure drop across it. The experimental values of Hensen (1895) for a No. 3 gauze (porosity, 0.44; strand diameter, 0.192 mm) are compared with values calculated from the equation of Wieghardt (1953).

by considering related investigations in fluid mechanics. Some work has been carried out on the flow associated with porous bodies, the investigations on the properties of the gauzes used in wind-tunnels being particularly relevant (Glauert *et al.*, 1932; Taylor and Davies, 1944; Simmons and Cowdrey, 1945; Schubauer *et al.*, 1950).

The relation between the flow through a gauze screen spanning a pipe or tunnel and the drop in pressure across the gauze is given by the equation

$$\Delta_P = K \cdot \tfrac{1}{2} \cdot \varrho V^2 \tag{1}$$

where Δ_P is the pressure drop, ϱ is the density of the fluid, V is the velocity of the flow, and K is the *resistance coefficient* (pressure-drop coefficient) of the gauze. Schubauer *et al.* (1950) showed that when the flow strikes the gauze at an angle θ *to the normal,* the pressure drop is determined by the normal component ($V \cos \theta$) of the approach velocity V. For angles of incidence up to 45°, it was observed that

$$\Delta_P \text{ (at angle } \theta) \approx K \cdot \tfrac{1}{2} \varrho (V \cos \theta)^2. \tag{2}$$

That is,

$$K_\theta \approx K \cdot \cos^2 \theta \tag{3}$$

K_θ being the resistance coefficient at the angle of incidence θ.

Now Wieghardt (1953) has shown that the value of K at zero angle of incidence is determined by β, the porosity of the gauze (see Terminology), and by Reynolds' Number (Re), the relation being of the form

$$K \approx \frac{1-\beta}{\beta^2} \cdot 6 \text{ Re}^{-1/3}. \tag{4}$$

Reynolds' Number is given by the equation

$$\text{Re} = \frac{V}{\beta} \cdot \frac{d}{\nu} \tag{5}$$

where d is the diameter of the strands in the gauze and ν is the kinematic viscosity (dynamic viscosity/density) of the water ($\nu \approx 0.01$). The effective Reynolds' Number becomes Re cos θ when the flow strikes the gauze at the angle θ to the normal.

The theory of the resistance of gauzes, as outlined above, would appear to be the basis on which a useful theory of filtration in plankton nets could be built. Schubauer's angle of incidence θ is equal to the side angle of a plankton net (see Fig. 2), and cos θ is equal to the ratio of the mouth area of a conical net (A) to the area of porous surface (a). The question is, how well do equations 1 to 5 describe the filtration performance of plankton nets according to our empirical observations?

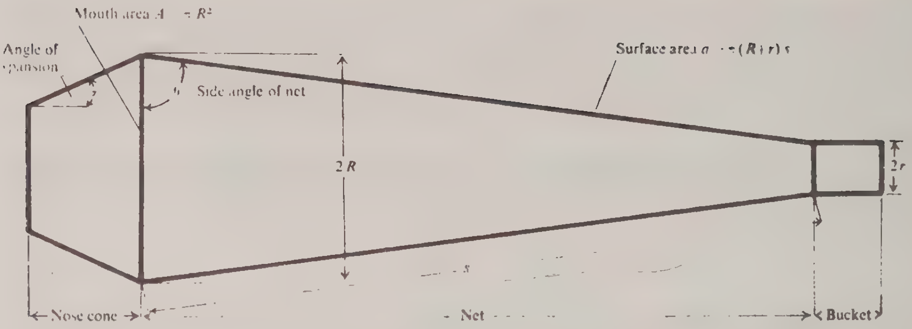

Figure 2
Generalized geometry of a plankton net with a mouth-reducing cone (after Tranter and Heron, 1967).
For a conical net, $A/a = \dfrac{\pi R^2}{\pi RS} = \cos \theta$.

The filtration efficiency of plankton nets shows a sharp decrease, in conformity with equation 3, when the side angle falls below about 75° or the ratio A/a rises above approximately 0.2 (Tranter and Heron, 1965, 1967; Smith *et al.*, 1964). However, at greater angles of incidence, this relation has only been shown to hold when all the water is channelled through the net (Sysoev, 1956); in plankton nets towed through the water, filtration efficiency shows little response to filtering area at these angles of incidence (Tranter and Heron, 1967). Tranter (1967) showed that filtration efficiency could be defined by the empirical equation

$$F \approx \frac{1}{1 + 0.01\,K} \qquad (6)$$

K being a function of the gauze porosity and Reynolds' Number (equation 4).

The filtration pressure (Δp) is determined not primarily by the towing velocity (V), but by the velocity (v) at which the water approaches the gauze (approach velocity). That is,

$$\Delta p = K \cdot \tfrac{1}{2}\,\varrho\, v^2. \qquad (7)$$

The approach velocity v (see Terminology) is related to the towing velocity V by the equation

$$v = V \cdot F \cdot A/a. \qquad (8)$$

The water approaching the gauze accelerates in transit through the meshes, the *mesh velocity* v' (see Terminology) being equal to v/β. It follows that

$$v' = V \cdot F \cdot A/a\beta. \qquad (9)$$

The factor $a\beta/A$ has been combined into the factor R (Smith *et al.**) which may be termed the *open area ratio* (see Terminology).

So far the discussion has been concerned with a 'simple' conical net. However, in most plankton nets there are other sources of resistance to flow through the net. Rings, bridles, flowmeters, mouth-reducing cones, casings, and so on produce what might be called *the resistance of the body of the sampler*. The effect of this resistance upon filtration efficiency must be determined empirically by towing the body of the sampler in a test tank and metering the flow.

The relation between the drag (D) of a plankton net and the velocity at which it is towed is given by the equation

$$D = C_D \cdot \tfrac{1}{2} \varrho V^2 A \tag{10}$$

where C_D is the *drag coefficient* of the net. There is little information on the drag coefficients of plankton nets. Motoda (1962*c*) used a drag coefficient of 1.33 to calculate the expected drag on the Indian Ocean Standard net. Wind-tunnel tests show that the value for the WP-2 net is also of this order (Tranter and Heron, unpublished data). In simple nets, C_D would appear to be related to the resistance coefficient of the gauze (K) but the nature of the relation has yet to be determined. The drag coefficient of complex samplers would have to be determined empirically.

It is doubtful if the theory outlined above can be developed further at the present stage unless attention were given to filtration performance under conditions of diminishing gauze porosity. It is now necessary to examine the consequences of the theory in practical plankton sampling.

PRACTICAL CONSEQUENCES

Flow patterns

The interaction between a plankton net and the water through which it is towed produces a pattern of flow which reflects some features of the net's filtration performance. This interaction affects the sampling process, in relation to the volume of water filtered by the net and the accuracy with which it is measured, the distribution of pressures at the filtering surface, and the warning given to motile zooplankton of the approaching net. The form of the net determines the volume filtered and the distribution of filtration pressure; the velocity profile across the mouth determines the optimum site for a flowmeter to be placed; and the solid structures used to tow and support the net, together with its own resistance, create the disturbances which might cause plankton to take avoiding action.

All the water at rest in the path of a plankton net is accelerated. At the gauze, water is accelerated around the strands and through the meshes. At the mouth, water is accelerated and displaced around the net (Fig. 3) as a consequence of resistance to the flow through the meshes. Ahead of the mouth, water is accelerated around the towing members, the energy dissipating in turbulence in their wake.

At the gauze. In a net at rest, the pressures either side of the gauze are equal. In a moving net, the pressure inside is increased by the flow of water entering the mouth.

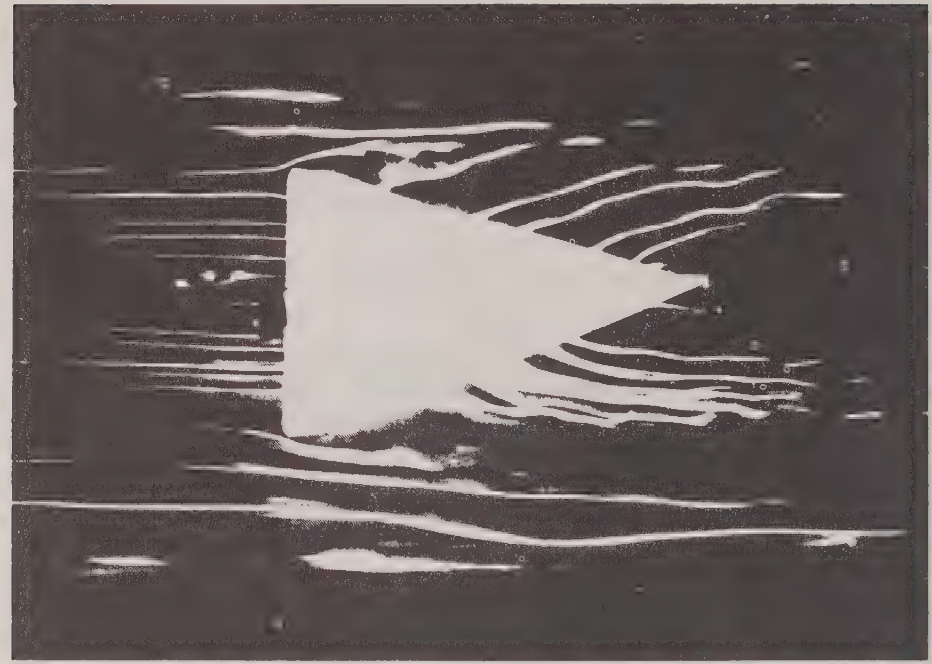

Figure 3
Flow pattern through a model plankton net (porosity 0.47 and side angle 70°). The streamlines are traced out in trails of smoke, and show the distribution of angular accelerations (from Tranter and Heron, 1967).

The resultant pattern of flow through the meshes is determined by the distribution of pressures along the inner and outer surfaces of the net. In a conical net, these pressures are rather evenly distributed and as a result the flow rate through the gauze is fairly uniform. Velocity transects (Tranter and Heron, 1967) show a slight reduction in flow at the throat of the net, but it is not clear whether this is the result of slower approach velocities or of the turbulence associated with the ring.

If a porous cylindrical section is added ahead of the cone, some of the water rejected by the cone is filtered through the cylinder (Currie, 1963). The filtering rate decreases forward from the point adjacent to the cone. In the CalCOFI standard net, 60 per cent of the gauze is in the cone and 40 per cent in a forward cylinder, and of the total water filtered, 3 per cent was filtered in the forward half of the cylinder (20 per cent of the gauze), 7 per cent in the after half of the cylinder, and 90 per cent in the cone (Smith and Clutter, 1965).

This has two consequences in the field. Since flow is evenly distributed over the cone, the probability of clogging is similar over the whole surface, and the addition of a forward porous cylinder (of the same gauze as in the cone) provides a potential filtering area which operates at an increasing rate as the cone clogs up. The second consequence is that the surface of the gauze in the forward cylinder oscillates, probably in response to eddies which would be shed alternately from the inner and outer peripheries of the net ring (Smith, Counts, and Clutter*; Halliday*). Smith and Clutter (1965) attribute the property of 'self-cleaning' to this oscillation.

The flow through the net approaches and leaves the gauze at a reduced velocity (Tranter and Heron, 1967) accelerating momentarily in transit through the meshes. Meanwhile the water deflected around the net is at near free-stream velocity. Tranter and Heron (1967) claim that this faster stream entrains the slower discharge. Enclosing a net within a non-porous cylindrical casing, for example, reduces the filtration efficiency of the net by approximately 40 per cent; part of this reduction could be due to the angular deformation of flow at the wall of the case.

At the mouth. Flow patterns at the mouth of a net are influenced both by the resistance of the net and by solid structures at, and forward of, the mouth. The mouth-reduction cone (such as on the Hensen Egg net, the Juday net, and most high-speed nets) increases filtration efficiency. As well as increasing the open area ratio, a reduction cone creates a low pressure area which draws a column of water wider than the reduced mouth through the sampler (Fig. 4*c*). Efficiencies higher than 130 per cent have been measured with the Hensen cone at 2.5 knots (Smith and Clutter, unpublished data). Tranter and Heron (1967) have used a flare behind the tube-mouth of the Clarke-Bumpus sampler to increase efficiency to 115 per cent.

Flow profiles across the entrance of large nets (Smith and Clutter, 1965; Jossi, 1966; Fraser, 1966; Mahnken and Jossi, 1967; Tranter and Heron, 1967) have shown the need to meter the flow at a site where the stream velocity is equal to the average through the entrance. In a net without forward bridles (Longhurst *et al.*, 1966) the centre position is probably representative. *Underestimates* would result if the flowmeter were placed behind solid structures such as the bridle apex or the closing apparatus (Jossi, 1966). Flowmeters outside the entrance of a net (Bé, 1962*a*; McGowan and Brown, 1966) would *overestimate* the flow through the entrance (Smith and Clutter, 1965) unless the net was fitted with a mouth-reducing cone. The magnitude of the error would depend on the filtration efficiency of the net and the degree of clogging. An overestimate would also be given in nets where the flowmeter is located at a coarse gauze section forward of the effective filtering surface, as in the Indian Ocean Standard net (Motoda, 1962*b*).

Ahead of the net. Flow patterns ahead of the net are represented here in two ways. In one method the trajectory of a parcel of water is represented by a line (streamline), and the rate at which adjacent lines diverge or converge is a measure of acceleration. By the other method, the magnitude and distribution of acceleration are represented directly.

Figure 4 illustrates the streamlines ahead of nets filtering at 75 per cent (Fig. 4*a*), 95 per cent (Fig. 4*b*), and 125 per cent (Fig. 4*c*) efficiency. Radial symmetry of flow is assumed, and each succeeding pair of lines from the centre adds another 10 per cent to the volume contained in a cylinder projected ahead of the entrance. The figures demonstrate that the consequences of filtration affect the water ahead of the net but not to great distances forward. The severity of angular deformation increases towards the rim, so influencing the capture of motile organisms (Fleminger and Clutter, 1965). Studies with mouth-reduction cones indicate that it may be possible

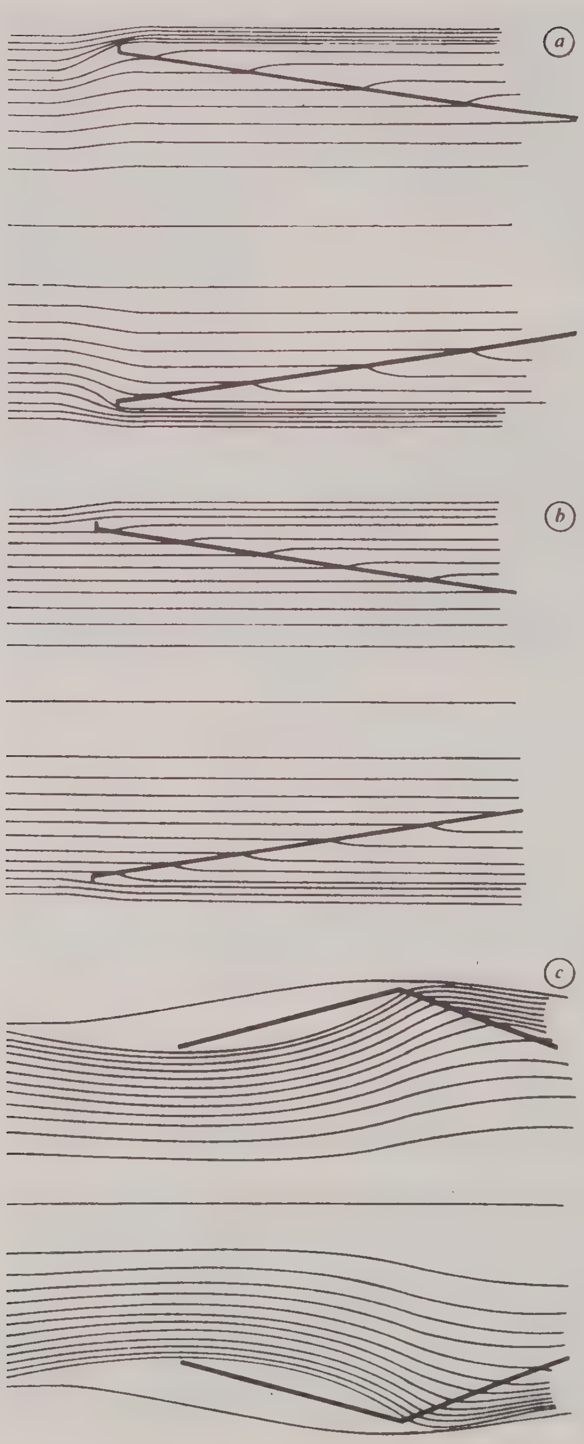

Figure 4
Streamlines ahead of nets. Each streamline encloses 10 per cent of the water entering a circular net.
a A conical net which is accepting 75 per cent of the water presented to it.
b A conical net which is accepting 95 per cent of the water presented to it.
c A conical net, with a mouth-reduction cone, which is accepting 125 per cent of the water presented to it.

to eliminate the forward consequences of the net's approach by enclosing the diverging streamlines to the point where they are parallel (filtration efficiency = 100 per cent). The main problem in this approach is the design of a filtering surface that will maintain the same filtering efficiency throughout the course of the tow (Smith, Counts, and Clutter*).

Accelerations caused by the resistance of the net do not extend so far forward as disturbances from solid objects such as the bridle, lead-line, cable clamp, and towing warp. In Figure 5 the disturbances caused by a non-filtering cone (Fig. 5*a*), bridle, lead-line, and rim (Fig. 5*b*), and the combination of a net and towing apparatus (Fig. 5*c*) are shown. Possible consequences of these forward flow disturbances are discussed more fully in Chapter 4.

Flow patterns in basic sampling systems. The flow patterns associated with most contemporary samplers have not yet been observed. In particular, there is insufficient information concerning the flow patterns associated with encased plankton nets. The patterns shown in Figure 6 are those which might be expected with several basic forms of design. They are based more on our present level of understanding than on patterns actually observed.

Filtration efficiency

The effect of filtering area. When the open area of an unencased net is less than three times the area of its mouth, filtration efficiency undergoes a progressive decline (Smith and Clutter, 1965; Tranter and Heron, 1965, 1967). When this ratio (R) is greater than 3, filtration efficiency tends towards a plateau. Although the lower filtration efficiency of short nets follows from the theory of inclined gauzes (see equation 3 above), its relative constancy in longer nets is not immediately obvious. Tranter and Heron (1967) suggest that the two components of the equation counteract each other; the trend towards lower resistance at greater angles of incidence ($\cos^2 \theta$) may be countered by the trend towards higher values of K at lower Reynolds' Numbers (equation 4). However, it is the effect of filtering area upon *sustained filtration efficiency*, rather than upon initial filtration efficiency, that is of greater consequence in practice.

Smith, Counts, and Clutter* showed that in natural waters the area of gauze in a net influences the duration of efficient filtration. With nets of nylon gauze, of mesh width 0.33 mm, and open area ratios 3.2, 4.8, and 6.4, the volume filtered efficiently was increased sixfold by doubling the filtering area (Table 1). This

TABLE 1. The effect of open area ratio on sustained filtration efficiency (F) (from Smith, Counts, and Clutter*)

Open area ratio	Volume filtered (m³) at $F > 85$ per cent	
	'Green' water	'Blue' water
3.2	49	390
4.8	123	1 172
6.4	300	2 564

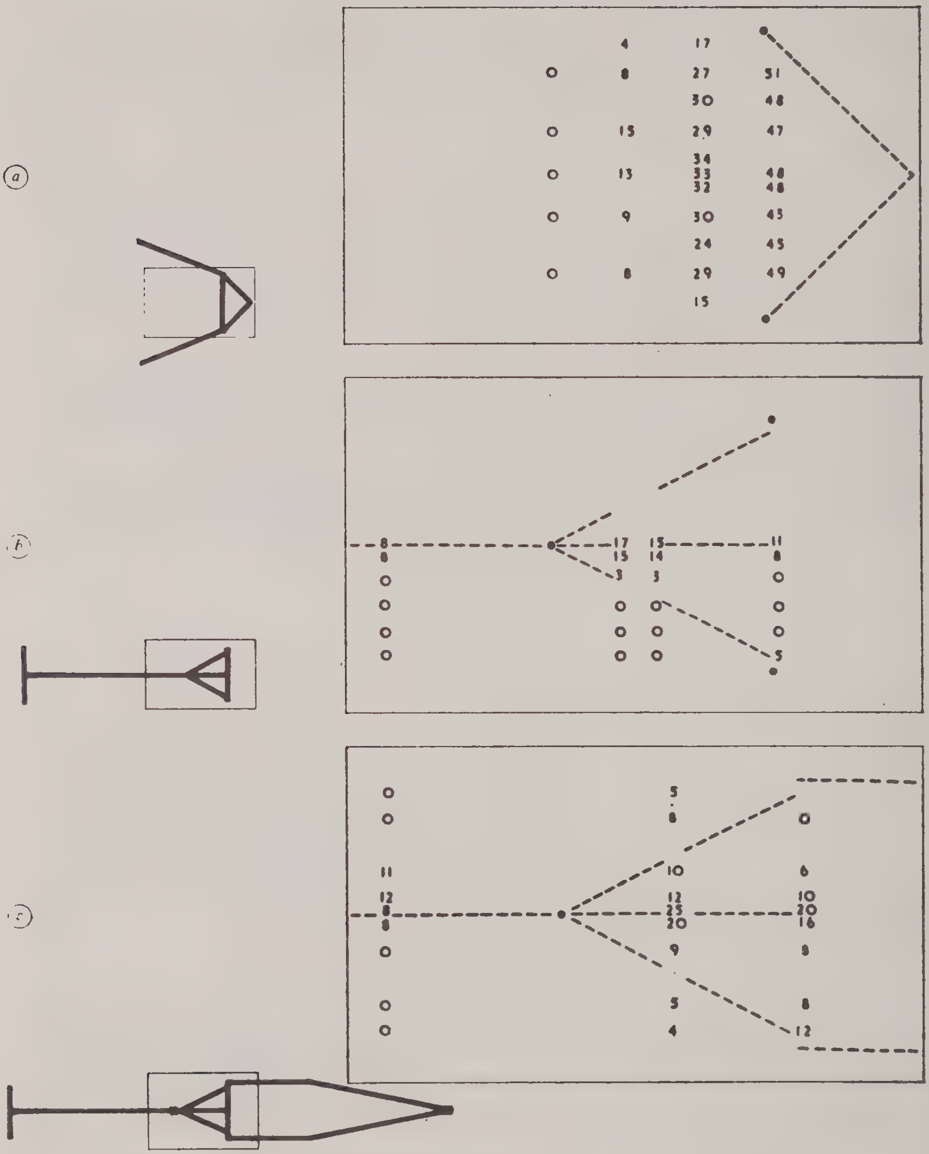
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Figure 5
The accelerations (cm/sec) ahead of plankton nets.
a Linear accelerations ahead of a non-filtering cone 1 m in diameter without a bridle preceding the entrance. The towing velocity is 77 cm/sec (1.5 knots).
b Linear accelerations ahead of a ring with bridle and lead line. The towing velocity is 129 cm/sec (2.5 knots).
c Linear accelerations ahead of a plankton net ring, bridle and lead line. The towing velocity is 129 cm/sec (2.5 knots) (after Smith and Clutter*).

augmented gain was attributed to 'self-cleaning' during the tow, clogging being the inevitable result of filtering natural waters (Kofoid, 1897*b*; Yentsch and Duxbury, 1956; Ito and Nishimura, 1958; Asaoka and Ohwada, 1960).

The porosity of the gauze and consequently the open area ratio of the net may also change from tow to tow. For instance, the porosity of the silk gauze used during the Plankton Expedition changed from 14 to 7 per cent due to shrinkage

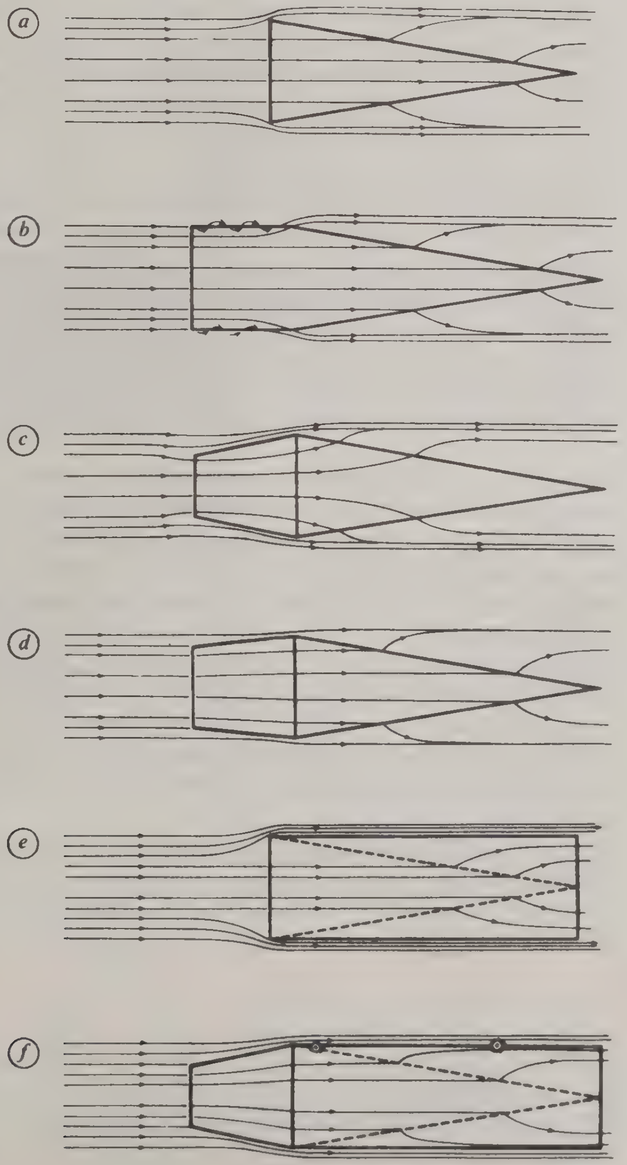


Figure 6
Probable flow pattern associated with some basic forms of plankton sampler.
a 'Simple' conical net ($F < 1$).
b Conical net with porous collar ($F \approx 1$).
c Conical net with non-porous mouth-reducing cone ($F > 1$).
d Conical net with non-porous mouth-reducing cone ($F = 1$).
e Conical net with non-porous casing ($F < 1$).
f Conical net with non-porous casing and non-porous mouth-reducing cone ($F = 1$).

]

and use (Hensen, 1895), and the open area ratio changed from 4:1 to 2:1. The effects of shrinkage on the mesh width and porosity of silk were described also by Ahlstrom (1948). Although monofilament nylon and metal gauzes do not shrink, they are more subject to the progressive accumulation of residual plankton (Ahlstrom, 1959), which dries more completely on monofilament than on multifilament strands, and is difficult to remove by routine washing procedures.

The effect of mesh size. According to the theory, the resistance of a piece of gauze is basically a function of its porosity and Reynolds' Number (equation 4 above). Experimental tows with nets of different porosity (Tranter and Heron, 1965) showed that the less porous nets filtered less water than the more porous nets (Table 2), particularly at low velocities ($<$ 1 knot). On the other hand, Smith and Clutter (1965) and Mahnken and Jossi (1967) could not find differences in filtration efficiency attributable to porosity alone.

In practice, however, fine gauzes clog more readily than coarse gauzes, and in this way mesh size does influence filtration efficiency (Smith, Counts, and Clutter*). In nets with the same area of gauze, the volume filtered before filtration efficiency is seriously affected appears to be a function of the square of the mesh width (Fig. 7). By this approximation, a net with a mesh width of 0.10 mm would clog 30 times faster than a net with a mesh width of 0.55 mm. The possibility of clogging cannot be excluded in the porosity experiments of Tranter and Heron (1965) even though the experimental tows were short (56 feet).

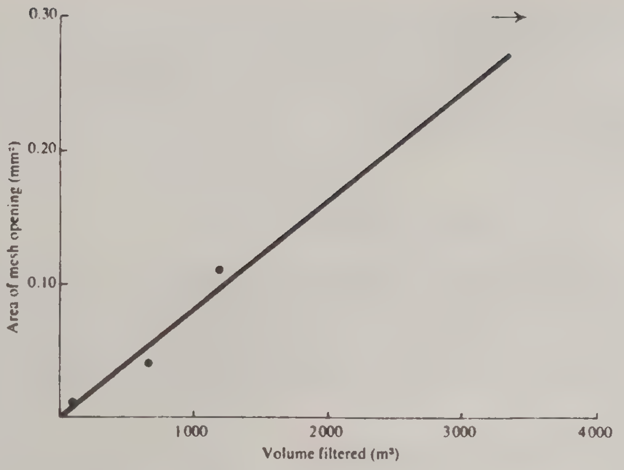
The effect of towing speed. The proportions of water filtered and rejected result from an equilibrium between the resistance of water to acceleration through the gauze and the resistance of water to lateral acceleration ahead of the net. Inertia and viscosity affect the resistance at both sites and at all velocities: at the *gauze* the contribution of viscosity to the resistance is relatively great and diminishes with increased speed, but at the *mouth* the contribution of viscosity to the resistance is relatively small and does not change appreciably. This results in a lower proportion of the water being filtered at lower speeds, particularly with fine gauzes.

At normal towing speeds ($>$ 1 m/sec) there is little effect on filtration efficiency (Bary *et al.*, 1958; Miller, 1961; Tranter and Heron, 1967). The magnitude of the speed effect can be gauged from the tests of Tranter and Heron (1965). The differ-

TABLE 2. The combined effects of mesh size and porosity on filtration efficiency (from Tranter and Heron, 1965)

Mesh width (mm)	Porosity	Open area ratio	Reduction in efficiency (per cent)
1.17	0.60	5.3	0
0.66	0.54	4.8	0
0.33	0.48	4.2	0
0.27	0.44	3.9	3
0.14	0.36	3.2	4
0.08	0.31	2.7	8
0.06	0.26	2.3	12

Figure 7
The effect of mesh width on clogging rate in which the area of the individual aperture is the ordinate and the volume filtered before filtration efficiency falls below 85 per cent is the abscissa. The mesh widths used are 0.10, 0.20, 0.33 and 0.55 mm, and the individual aperture areas are 0.01, 0.04, 0.11 and 0.30 mm^2. The coarsest gauze had not clogged at the end of the test (Smith, Counts, and Clutter*).



ences observed ranged from 3 to 4 per cent for gauzes ranging in mesh width from 0.27 to 1.17 mm and from 6 to 12 per cent for mesh widths of 0.06 to 0.14 mm, the greater part of the difference occurring below towing velocities of 0.6 m/sec (1.2 knots). Because low towing speeds might be adopted more commonly in future to improve the condition of the catch, these experiments should be repeated, preferably using a flowmeter with a low friction point.

Filtration pressure

It has often been observed that plankton organisms are taken in poorer condition at high towing velocities. For instance, Tranter, Kerr, and Heron* recorded progressive damage to Appendicularia between hauling speeds of 1.5 and 2.4 m/sec. Since velocity is unlikely to cause any direct damage, this is generally attributed to the associated pressure drop across the meshes. It is likely that this filtration pressure also influences the selectivity of organisms by the meshes (Vannucci: see Chapter 5 below); Hensen (1895), for example, found that a net with a high filtration pressure caught only two-thirds as many small copepods as a similar net with a low filtration pressure.

However, the pressure drop across the meshes of a plankton net has never been measured. It is therefore necessary to seek some understanding of the parameters of filtration pressure from the theory available. Hensen (1895) was the first to state the basic relationship

$$\Delta p = K \cdot \tfrac{1}{2} \varrho \cdot v^2$$

between the velocity, v, at which a stream of water approaches a gauze, and Δp, the resultant pressure drop across it. Because this pressure varies, not as a linear function of the approach velocity, but *as the square of the approach velocity*, small changes in velocity will lead to relatively large changes in filtration pressure. The approach velocity is related to the velocity at which the net is towed, the filtration efficiency of the net, and the ratio of the mouth area to the area of gauze in the net (equation 8 above).

This field is one in which more work is needed. In particular, there should be systematic investigations on the effect of filtration pressure on the retention of organisms by the gauze.

PLANKTON NET DESIGN

The area of gauze in a plankton net should be large enough to filter water efficiently. Fine nets which are to sustain filtration for a long time need reserve filtering area to maintain high efficiency. High-speed nets need an area of gauze large enough to reduce the pressure exerted on the organisms caught to within an acceptable limit.

Initial filtration efficiency

In practice, the initial filtration efficiency of unencased nets is determined by their open area ratio (see 'Theoretical basis' above) regardless of mesh size and towing speed. The minimum open area ratio has not been generally determined for a range of mesh sizes, but it appears that any simple conical net made from a modern gauze would filter at more than 85 per cent efficiency provided the open area ratio were greater than 3; nets with an open area ratio greater than 5 could filter at up to 95 per cent efficiency. Ratios higher than this are unlikely to yield much higher efficiencies unless a mouth-reducing cone is used (Fig. 4*c*, 6*c*). Reducing cones are more efficient when their angle of expansion (see Fig. 2) is small (Tranter and Heron, 1967); for top efficiency the angle should be less than 3½° (Pankhurst and Holder, 1952).

The first step in plankton net design is to determine the grade of gauze necessary to retain the organisms desired (see Vannucci, Chapter 5 below). The porosity of the chosen gauze should then be determined. This specification is usually available from the distributors, but it can also be obtained by direct measurement (see Terminology) either with an eyepiece micrometer or by polar planimetry of photo-

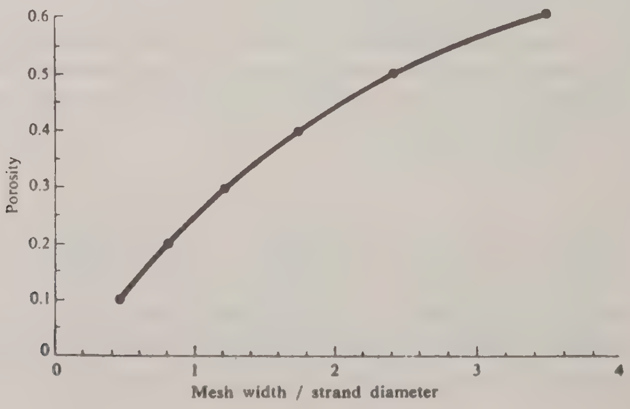


Figure 8
A graphic method of estimating porosity from the ratio of the mean mesh width to the mean strand diameter.

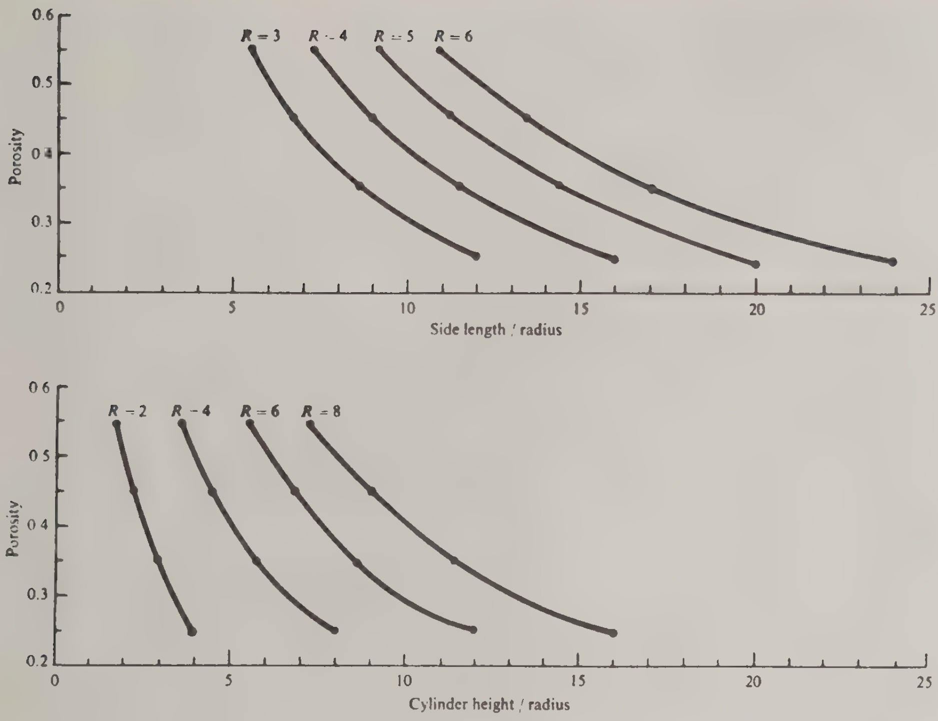


Figure 9
a A graphic method for estimating the cone side length for nets with open area ratios of 3 to 6 where the gauze porosity is between 0.25 and 0.55. The units on the abscissa are to be multiplied by the radius to determine side length.
b A graphic method for estimating the cylinder height of the reserve mesh to be added to a net for open area ratios of 2 to 8. The units on the abscissa are to be multiplied by the radius to determine cylinder height.

graphs or drawings. Figure 8 shows the approximate relation between porosity and the ratio of mesh width to strand diameter. Given the porosity, the desired open area ratio may then be selected using Figure 9. The radius of the mouth entrance will be determined by other considerations, such as the volume to be sampled (see Cassie, Chapter 7 below), the avoiding reactions of the organism sought (see Clutter and Anraku, Chapter 4 below), or the limitations due to drag (see Gehringer and Aron, Chapter 6 below).

Sustained filtration efficiency

Having established the requirements for a particular filtration performance, features should then be included in the design to ensure that this performance will be sustained throughout the haul or tow. The problems of sustaining filtration efficiency are not well defined for the entire range of grades of gauze. We make the general recommendation that a cylinder of gauze be added to the terminal cone. The cylindrical collar withstands clogging better than the cone (Smith, Counts, and Clutter*) and adds less to the over-all length of the net than the same amount of filtering area in a conical form. An over-all open area ratio of 5, with 3 in the cone and 2 in the cylinder, would be a satisfactory starting point for gauzes of mesh width greater than one-third of a millimetre. For mesh widths smaller than this, an over-all open area ratio of 9, with 3 in the cone and 6 in the cylindrical collar would probably be satisfactory, at least for low speed tows of less than 20 minutes' duration. This information is summarized in Figure 9.

The importance of clogging in a given region or season is not yet predictable. Smith, Counts, and Clutter (unpublished data) found by extrapolation of clogging results from nets with a mesh width of 0.333 mm and open area ratios of 3.2, 4.8, and 6.4, that a net of open area ratio 7.8 would be likely to withstand a tow of 750 m in a neritic zone.

There are no data with which to predict the clogging of high-speed nets.

Control of filtration pressure

Because it is determined by the velocity at which the water approaches the immediate vicinity of the gauze (see page 41), filtration pressure may be controlled not only by varying the velocity at which the net is towed but also by varying the open area ratio of the net. In encased samplers this ratio may be increased either by increasing the area of the net or by reducing the size of the entrance to the case: the latter principle is basic to the design of high-speed samplers. In unencased samplers, on the other hand, the ratio can best be increased by increasing only the area of the net; mouth-reductions in unencased nets are to some extent self-defeating, their effect being to increase the effective area swept by the smaller mouth (Fig. 4*e*).

There is not enough information on the levels of filtration pressure, or upon their effects, to specify standards. These must ultimately be set by the practising planktologist.

Laboratory and field testing

Test tanks ('ship tanks') and wind-tunnels are standard equipment in hydrodynamics and aerodynamics laboratories and are well suited for testing plankton samplers. Flow patterns in air are directly comparable with those in water, provided allowance is made for the different kinematic viscosities of air and water (Alexseev, 1964; Miyazaki, 1964; Tranter, 1967).

The test tank is an open water channel through which instruments may be moved at predetermined velocities. Usually a pair of rails straddles the channel, and on these runs an electric trolley from which the sampler may be suspended by a vertical boom.

In many respects wind-tunnels are more convenient for testing plankton samplers. Air is drawn continuously through the tunnel by a fan, delivering an even stream of air through a working section with a viewing window. The sampler is

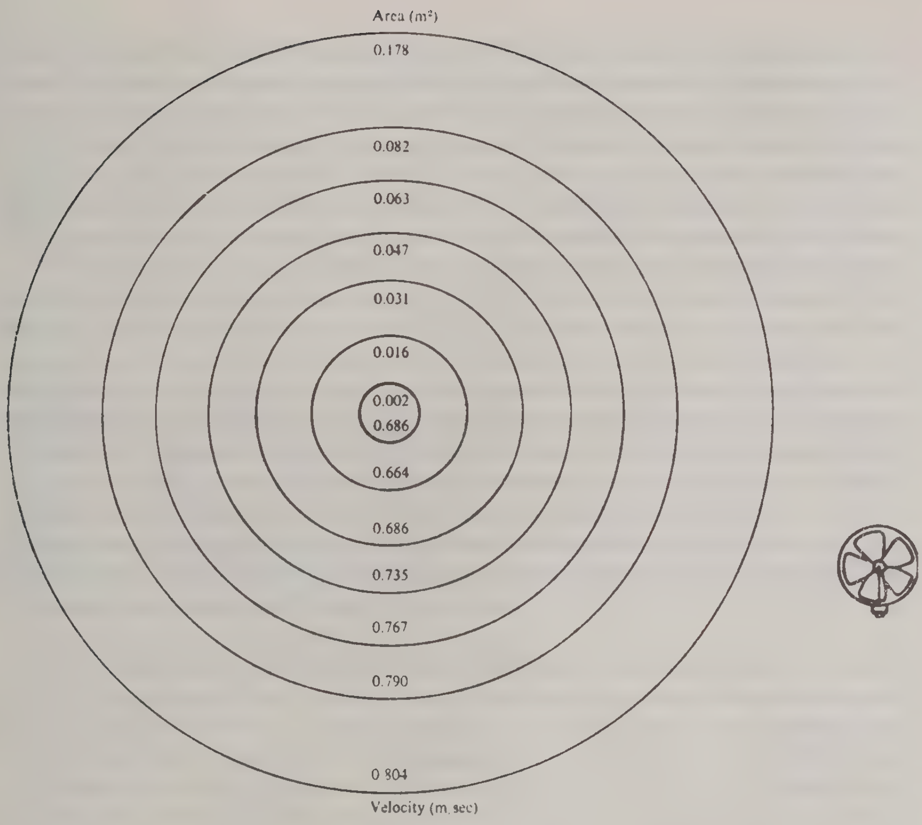


Figure 10
Diagram for computing the filtration efficiency of a net using the flow velocity transect method. The flowmeter is drawn to scale at the right. To convert from flow velocity to volume, the velocity is multiplied by the area it is intended to represent, assuming radial symmetry of flow (see Table 3).

suspended in the centre of the working section facing the airstream, and its properties are measured by probes inserted through the top or side of the tunnel: the pitot tube may be used to measure pressure; the hot-wire anemometer to measure velocity and turbulence; a mechanical balance to measure the drag of the net and its associated components; and the flow pattern may be observed by means of jets of smoke liberated upstream of the net (Fig. 3) or by tufts of thread attached at various points. The wind-tunnel may also be used to investigate the properties of towing warps (Alexseev, 1964) and depressors.

Filtration efficiency. The filtration efficiency of plankton samplers has been determined in irrigation canals (Smith and Clutter, 1965), in recirculating water channels (Mahnken and Jossi, 1967; Smith and Clutter*), in towing tanks (Tranter and Heron, 1965, 1967), in wind-tunnels (Tranter and Heron, 1967), and at sea (Currie and Foxton, 1957; Bary *et al*., 1958).

The basic technique for samplers with flowmeters which are large relative to the net entrance is to tow the sampler, with and without a net attached, over a known distance, metering the discharge through the mouth of the sampler in each case. The main factors influencing the accuracy and precision of the determination are the flowmeter, the measure of distance, and the presence of clogging during the test trial (Tranter and Heron, 1965). If the trials are at a velocity near the friction point of the flowmeter, care must be taken to use a flowmeter calibration appropriate to the velocity of the water through the entrance with the net attached.

The flow transect is the basic technique for measuring filtration efficiency of samplers with flowmeters which are small relative to the mouth of the sampler. First, the flow in the test section is measured at intervals, without the net in place, to ensure that flow is distributed evenly. The net is then installed and a similar flow transect taken. Figure 10 shows the velocity profile of the flow through the mouth of the Hensen Egg net; the channel velocity is 0.718 m/sec (1.4 knots). The diameter of the net is 0.73 m, and the diameter of the flowmeter is 0.076 m. Thus each meter reading directly represents only 1 per cent of the mouth of the net. If one assumes radial symmetry of flow through the mouth, each meter reading represents the area of a ring defined by the radius divided by the number of meter sites. In this instance, the flow at 30 cm from the centre (Table 3) represents 143 times as much volume as the flow at the centre; this proportion would vary with the number of metering sites chosen and with the mouth size. Table 3 shows that the mean velocity through the net mouth was approximately 0.773 m/sec, and that the flowmeter site which most closely represented this was 20 cm from the centre. The sum of the results of multiplying the velocity by the area represented by that site gives an estimate of the volume being filtered each second. At this velocity, the net is estimated to be 107 per cent efficient. By a similar process, filtration efficiency could be determined with several flowmeters installed in the mouth of the net at various distances from the centre.

TABLE 3. An example of the flow transect method of determining filtration efficiency[1]

Distance of flowmeter from centre (cm)	Radius represented (cm)	Area represented (m^2)	Velocity (m/sec)	Volume represented (m^3/sec)
Centre	0—2.5	0.002	0.686	0.001
5	2.5—7.5	0.016	0.664	0.011
10	7.5—12.5	0.031	0.686	0.021
15	12.5—17.5	0.047	0.735	0.035
20	17.5—22.5	0.063	0.767	0.048
25	22.5—27.5	0.082	0.790	0.065
30	27.5—36.5	0.178	0.804	0.143
		0.419		0.324

[1] Channel velocity = 0.718 m/sec; mean velocity through net entrance = 0.773 m/sec.

Clogging. The effects of clogging may be studied either in the laboratory or in the field. In the field, clogging can be tested using ordinary flowmeters, one mounted inside and another outside the rim. It should be borne in mind that the rate of the outer flowmeter could increase as the rate of the inner one decreases, due to acceleration of displaced water around the net. We suggest that the ratio of these readings be determined by several trials; at the normal duration of the tow, half the duration of tow, and twice the duration of tow. Preferably these trials should be conducted in areas known to yield high concentrations of plankton, and should be repeated after the nets have been in use for some time to detect differences due to shrinkage or to reduced porosity. The progress of clogging during a tow can be observed by telemetering the flow rate to the ship. It is also possible to record flow rate *in situ* for later examination (Currie and Foxton, 1957; Longhurst *et al.*, 1966).

Filtration pressure. The filtration pressures generated by a net are an essential consideration in the design of plankton samplers. Because Hensen's values are too high (see Fig. 1), it would be useful to repeat his work using modern silk gauzes, and those made from synthetic fibres and from metal. In particular, the equation of Wieghardt (1953), on which the present estimates of filtration pressure are based, needs to be confirmed for the gauzes usually used in plankton nets. However the greatest need of all is to determine in greater detail the effects of pressure on mesh selectivity and specimen condition.

Forward disturbances. Advance warning to motile zooplankton may well reduce the accuracy of plankton sampling (see Clutter and Anraku, Chapter 4 below). Some of the forward disturbances caused by the net and the towing apparatus can be measured in the laboratory. These may be divided into linear acceleration, angular acceleration, and turbulence. Linear accelerations may be estimated from flow transects forward of the mouth, but interpretation becomes more difficult in the presence of angular accelerations. These may be shown by classical techniques involving yarn tabs, dye trails, and smoke streams (see Fig. 3). Turbulence is likely to be important in stimulating small plankton organisms because the fluctuations of small-scale accelerations are greater than the onset of large-scale accelerations caused by the approach of the net. The hot-wire anemometer is a suitable instrument for measuring turbulence in air.

Net construction

Two forces interact to reduce oscillation of the filtering surface during the tow: the force of the water at right angles to the gauze, and the drag of the net which is parallel with the towing direction and acts on the longitudinal dimension of the net. The filtering pressure is kept low by design and is fairly evenly distributed over the gauze. However, the drag is additive from the posterior to the anterior part of the net. For this reason, longitudinal support webbing is required to relieve the tension on the gauze. Figure 11 shows the drag on the support ring of nets with mouth areas of 0.1 m^2 to 2.0 m^2, at towing velocities of 1 to 18 knots (0.5 to 9.5 m/sec). A minimum of four support webs, short enough to allow slack in the gauze, should be placed evenly on the circumference of the net to run its entire length. Nets with a mouth area of 1 m^2 or more should have eight such webs. Transverse webs should

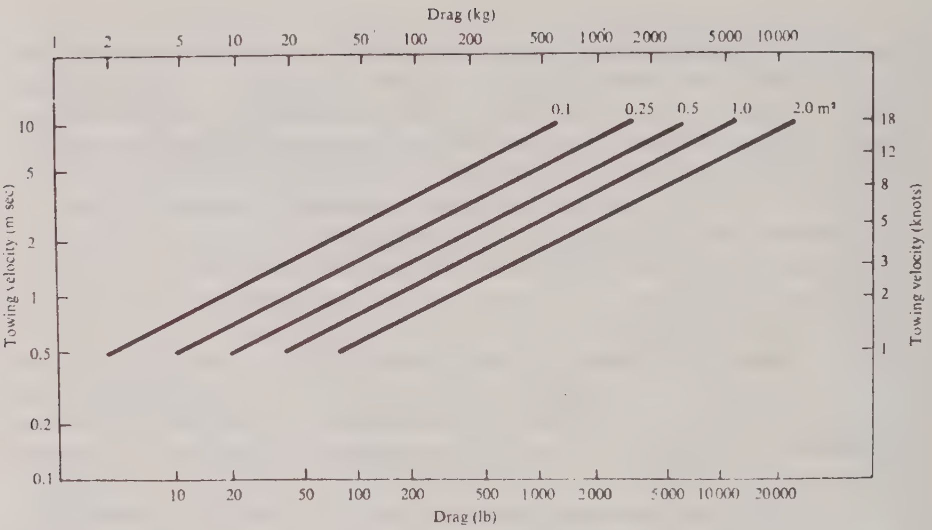


Figure 11
A graphical method for estimating the drag of nets with mouth areas of 0.1 to 2.0 m², towed at velocities of 0.5 m/sec (1 knot) to 9.50 m/sec (18 knots), assuming a drag coefficient of 1.33 (from Motoda, 1962).

not be used, as they stop the longitudinal oscillations of the filtering surface and are a site of plankton accumulation during the tow (Smith and Clutter, 1965).

CONTEMPORARY SAMPLERS

The diversity of nets in common use reflects the wide range of plankton species sought and the type of problems the nets are meant to solve. Most nets have not been tested thoroughly, either in the laboratory or in the field. We have attempted below to assess the probable filtration performance of a number of samplers whose specifications have been given in sufficient detail. In doing so, we would emphasize that assessments of this sort are an inadequate substitute for actual tests and should be checked against empirical observations whenever these can be obtained.

We have arbitrarily divided these samplers (Table 4) into high-speed (> 3 knots) and low-speed (< 3 knots) nets, with coarse (> 0.4 mm), medium (0.2-0.4 mm), and fine (< 0.2 mm) gauzes. Within each category, the nets are listed in decreasing order of open area ratio. An estimate of their initial filtration performance can be gauged from Tables 5 and 6.

Low-speed nets

These are taken to include those nets towed at less than 150 cm/sec, with the ship manoeuvred to maintain a vertical towing wire, adrift with a varying wire angle, or under way near its lower limit of speed to maintain a constant wire angle. In Table 5, values are given for the filtration efficiency, mesh velocity, approach velocity (and associated dynamic pressure), and filtration pressure, in some unenclosed nets with unreduced mouth openings and uniform mesh size. For the purposes of comparison, all the values are based on a towing velocity of 100 cm/sec (2 knots), but the towing velocities that would yield approach velocities of 5, 10, 15 and 20 cm/sec are also given.

The values in Table 5 are based on the resistance coefficient equation of Wieghardt (1953) and the filtration coefficient equation of Tranter (1967) (see 'Theoretical basis' above), assuming an even distribution of velocity and filtration pressure at all points on the filtering surface. Where nets have both cylindrical and conical sections, the values for the cylinder will be much lower, and the values for the cone much higher, than the average given here. If more accurate values of filtration efficiency are known from empirical observations, they should be substituted in the table to yield more accurate values of filtration pressure and mesh velocity.

The mesh velocities range from approximately 10-50 cm/sec and the filtration pressures from approximately 0.1-1 g/cm^2, the CalCOFI Anchovy Egg net and the Bongo net being at the lower end of the range, and the Marutoku nets at the higher. The table shows a parallel variation in the particular towing velocity which should be used to achieve a particular filtration performance. Some of the samplers could be towed at a much faster rate than 100 cm/sec while others should be towed more slowly. Because the cylinder-cone nets do not have an even pressure distribution at all points on the gauze, they are not suitable for an extension of the speed range without rearranging the proportions of gauze in the cone and cylinder.

It should be remembered that Table 5 indicates *initial* filtration performance only. The filtration performance at the end of a tow could be very different, depending on the fineness of the gauze, the open area ratio, the duration of the tow, and the plankton concentration in the water.

Coarse gauzes. The combination of large mesh size and high open area ratio (6.8) in the Bongo net would make clogging unlikely. The FAO larval tuna net (Matsumoto, 1967) was designed to filter 1,500 m^3 of water at high efficiency, the mesh width being set at 0.5 mm (diagonal 0.7 mm); this net is not likely to clog because of the forward potential filtering section. Tests on the Interim net designed by WP-3 of the ICES-SCOR-Unesco Working Group on Zooplankton Sampling Methods (Smith, unpublished data) showed that it could filter 1,900 m^3 of California Current water without clogging. The CalCOFI net (Ahlstrom, 1948) has a cylinder-cone shape, the mesh width (0.55 mm) being a compromise between the two sizes used in earlier nets (0.3 and 0.7 mm), to collect pelagic fish eggs and larvae; the probability of clogging is low in standard tows (15 minutes, oblique, from 140 m) but the net may not be able to withstand sustained towing in neritic surface waters.

Medium gauzes. The CalCOFI Anchovy Egg net was designed to filter 125 m^3 of neritic water without change in filtration efficiency (Smith, Counts, and Clutter*); there has been no evidence of clogging in 2,000 15-minute tows in the California Current; the filtration pressure is low initially, but may rise considerably if clogging should reduce the open area ratio. The catch of the Australian Clarke-Bumpus

TABLE 4. Some contemporary nets

	Mouth area (m^2)	Form	Mesh width (mm)	Porosity	Open area ratio	Reference
		LOW-SPEED NETS (< 3 KNOTS)				
Coarse gauze (> 0.4 mm)						
Bongo net	0.38	Cone	0.51	0.51	6.8	McGowan and Brown, 1966
FAO-Larval tuna	0.79	Cyl-cone[1]	0.51	0.51	4.8	Matsumoto, 1966
WP-3 (Interim)	1.00	Cyl-cone	1.00	0.58	3.7	Fraser, 1966
CalCOFI Standard	0.79	Cyl-cone	0.55	0.36	3.2	Smith *et al.* *
Tropical Juday—large	1.00	Red-cone[2]	0.45	0.40	3.1	Bogorov, 1959
Medium gauze (0.2–0.4 mm)						
CalCOFI Anchovy Egg	0.20	Cyl-cone	0.33	0.46	7.8	Smith *et al.* *
Australian Clarke-Bumpus	0.012	Cone	0.27	0.44	5.3	Tranter, 1965
Indian Ocean Standard	1.00	Cyl-cone	0.33	0.46	4.3	Currie, 1963
NORPAC net	0.16	Cone	0.35	0.46	3.7	Motoda and Osawa, 1964
ICITA	0.79	Cone	0.28	0.42	3.1	Jossi, 1966
Marunaka	0.28	Cone	0.33	0.45	2.4	Nakai, 1962
Hensen Egg	0.42	Red-cone	0.30	0.44	2.1	Künné, 1933
Marutoku A	0.16	Cone	0.33	0.45	1.7	Nakai, 1962
Fine gauze (< 0.2 mm)						
WP-2	0.25	Cyl-cone	0.20	0.45	6.0	Fraser, 1966
Tropical Juday-Reg	0.50	Red-cone	0.17	0.32	4.2	Bogorov, 1959
Kitahara	0.05	Red-cone	0.11	0.32	4.2	Nakai, 1962
Flowmeter	0.38	Cyl-cone	0.17	0.32	3.2	Currie and Foxton, 1957
Bé net MPS	0.25	Pyramid	0.20	0.45	2.7	Bé, 1962*a*
Marutoku A	0.16	Cone	0.11	0.32	1.2	Nakai, 1962
Mixed gauzes						
International Standard	0.20	Cone	10.00 0.23 0.08	 0.36 0.20	2.6	Ostenfeld and Jespersen, 1924
N 70	0.37	Cone	10.00 0.37 0.17	 0.34 0.32	2.4	Foxton, 1956

		HIGH-SPEED NETS (> 3 KNOTS)				
Coarse gauze (> 0.4 mm)						
Miller high speed I	0.0081	Red-cone[2]	0.95	0.57	28.0	Miller, 1961
Jet net	0.0110	Red-cone-Enc[3]	0.44	0.48	27.0	Clarke, 1964
Miller high speed II	0.0081	Red-cone	0.53	0.52	26.0	Miller, 1961
Medium gauze (0.2–0.4 mm)						
Miller high speed II	0.0081	Red-cone	0.26	0.44	22.0	Miller, 1961
Gulf III modified	0.0320	Red-cone-Enc	0.38	0.44	13.1	Bridger, 1958
Hardy recorder	0.00016	Red-disc-Enc	0.22	0.37	11.8	Glover, 1953
Isaacs high speed	0.0005	Red-cyl-Enc	0.24	0.30	11.2	Ahlstrom *et al.*, 1958
Catcher	0.0410	Red-cone-Enc	0.46	0.55	11.0	Bary *et al.*, 1958
Hardy sampler	0.00029	Red-cone-Enc	0.22	0.37	8.1	Glover, 1953
Gulf III	0.1300	Red-cone-Enc	0.38	0.44	3.2	Gehringer, 1952
Small Hardy indicator	0.00013	Red-disc-Enc	0.22	0.37	2.3	Glover, 1953
Standard Hardy indicator	0.0011	Red-disc-Enc	0.22	0.37	1.4	Glover, 1953
Fine gauze (< 0.2 mm)						
Jashnov high speed	0.25	Pyramid	0.17	0.32	1.9	Jashnov, 1961

1. Cylinder-cone.
2. Reduction cone-cone.
3. Encased gauze section.

Table 5. Initial filtration performance of some contemporary samplers, calculated from the equations of Wieghardt (1953) and Tranter (1967)

Plankton sampler	Towing velocity: 100 cm/sec					Towing velocity which will give an approach velocity of:			
	Filtration efficiency (F)	Mesh velocity (v')	Approach velocity (v)	Dynamic pressure at v cm/sec ($\frac{1}{2} \varrho v^2$)	Filtration pressure ($K \cdot \frac{1}{2} \varrho v^2$)	$v = 5$	$v = 10$	$v = 15$	$v = 20$
		(cm/sec)	(cm/sec)	(g/cm^4)	(g/cm^2)	(cm/sec)			
Bongo	0.96	14	7	0.027	0.097	69	138	207	276
FAO Larval Tuna	0.97	20	10	0.054	0.176	49	97	146	194
WP-3 Interim	0.98	26	15	0.120	0.239	33	65	98	130
CalCOFI Standard	0.91	29	10	0.054	0.383	48	97	146	194
CalCOFI Anchovy Egg	0.95	12	6	0.016	0.089	90	179	269	358
Australian Clarke-Bumpus	0.88	17	7	0.027	0.158	52	104	156	208
Indian Ocean Standard	0.96	22	10	0.053	0.244	49	98	147	196
NORPAC	0.96	26	12	0.072	0.309	42	84	126	168
ICITA	0.95	31	13	0.084	0.456	39	78	117	156
Marunaka	0.88	37	16	0.138	0.553	30	61	91	121
Marutoku A (medium)	0.80	47	21	0.228	0.817	24	47	71	94
WP-2	0.94	16	7	0.025	0.161	71	142	213	284
Flowmeter	0.90	28	9	0.041	0.476	56	112	167	223
Bé Multiple	0.88	33	15	0.110	0.534	34	68	102	136
Marutoku A (fine)	0.59	49	16	0.125	1.237	32	64	96	128
Jashnov	0.78	41	13	0.089	0.871	38	76	113	151

(Tranter, 1965) compares favourably with that of the much larger Tropical Juday net and Indian Ocean Standard net (Barnes and Tranter, 1965); the filtration efficiency is only 4.6 per cent lower than in the sampler without a net (Tranter and Heron, 1965); clogging has been reported with other Clarke-Bumpus samplers (Yentsch and Duxbury, 1956; Regan, 1963) and in other mesh sizes; based on tests with nets of similar proportions, the sampler might begin to clog after filtering approximately 16 m^3 of oceanic water and 4 m^3 of neritic water.

The filtration efficiency of the Indian Ocean Standard net (Currie, 1963) has been measured at 70-90 per cent (Motoda *et al.*, 1963) but these figures are probably a little low; the net is not likely to clog when hauled vertically in central water masses, but may do so when the wire-angle is high or the water rich in plankton. The ICITA net (Jossi, 1966) was adopted as a general purpose net for oblique tows from 200 m in tropical waters; tests on analogous conical nets indicate a high probability of clogging in tows longer than 10 minutes, in all but the central water masses. The Marunaka and Marutoku nets (Nakai, 1962) are used in brief vertical tows; their initial filtration efficiency is low and would rapidly decrease with clogging. The Hensen Egg net (Table 6) was also designed for brief vertical tows; due to its reduction cone (see 'Practical consequences' above) the initial filtration efficiency is greater than 100 per cent but the low open area ratio (2.1) and the small mesh size make this net extremely sensitive to clogging; this would increase the filtration pressure and raise the mesh velocity through the remaining apertures.

Fine gauzes. The WP-2 net (Fraser, 1966) was designed to be hauled vertically from 200 m in the open ocean, and from near bottom to the surface on the continental shelf; tests on the prototype (Smith, unpublished data) showed that its initial filtration efficiency (94 per cent) dropped to 38 per cent after 5 minutes' towing at 2.3 knots (Fig. 12); as a result of the tests, the open area ratio was increased from 5 to 6 (Fraser, 1966) and it was recommended that two flowmeters be used to monitor clogging, one inside and one outside the entrance. The Tropical Juday net (Bogorov, 1959) and the Kitahara net (Nakai, 1962) have similar open area ratios (4.2); the initial filtration efficiency probably exceeds 100 per cent (due to the reduction cone) and the probability of clogging would be high in tows longer than 50 m in waters rich in plankton. The Flowmeter net (Currie and Foxton, 1957) is used for vertical tows, and has given no sign of a decrease in filtration efficiency attributable to clogging. The Bé multiple plankton sampler (Bé, 1962*a*) is usually used in a descending oblique tow, the entire net being changed within the entrance at preset depths; there would be an interaction between adjacent nets but the effect of this is difficult to predict; the filtration pressure would be relatively high and the particular net which samples the upper layer would be sensitive to clogging. The filtration efficiency of the Marutoku A net (Nakai, 1962) would be very low, and would rapidly decrease as the net clogs (Ito and Nishimura, 1958).

Mixed gauzes. The ICES Standard net would have an initial filtration efficiency of approximately 80 per cent; however, Gibbons and Fraser (1937*b*) found the net to be only 56 per cent efficient after filtering 3.5 m^3 of neritic water containing *Ceratium*. The initial filtration efficiency of the Discovery N70 net (Foxton, 1956)

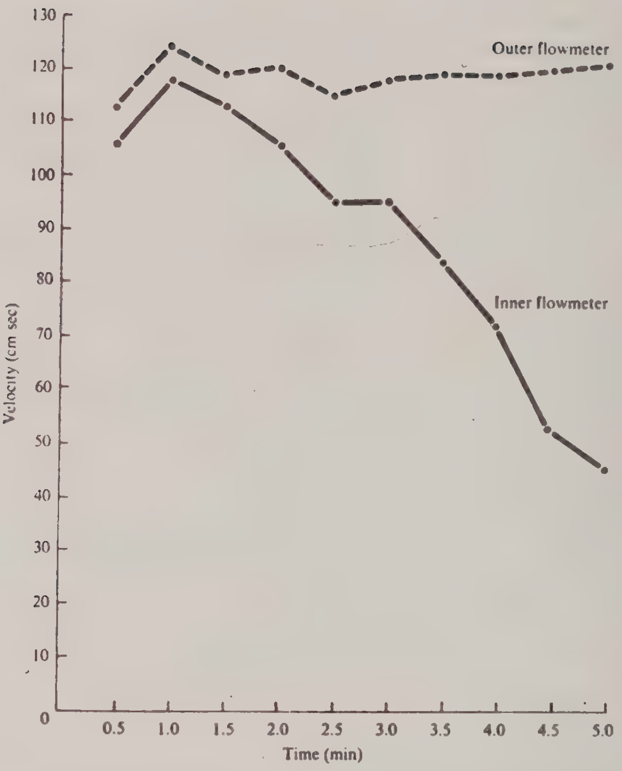


Figure 12
The clogging rate of an early model of the WP-2 net (Fraser, 1966) being towed at 120 cm/sec in neritic water off San Diego, California. Clogging is indicated by the progressive decrease in the velocity of the water through the mouth of the net.

is probably of the same order, and the posterior section of fine gauze (0.17 mm) is equally likely to clog.

The filtration performance of such nets is not well understood, particularly the effect of clogging in the finer part upon filtration in the coarser part. Presumably, as the fine gauze clogged the coarse part would progressively become the effective filtering surface, and the velocity of the water through the coarse meshes would increase. It is more difficult to nominate the consequent effect upon filtration pressure at various sites of filtration.

The usefulness of nets made from more than one gauze has yet to be clearly demonstrated. Sometimes a coarse gauze is used around the throat of the net to hasten its rate of descent, as in the Indian Ocean Standard net, but there could well be other equally satisfactory solutions to this logistic problem. Until much more is known about the complexity of their filtration performance, we would recommend that nets with mixed gauzes should be replaced by nets with a uniform gauze throughout.

High-speed nets

The filtration performance of contemporary high-speed nets is less well understood than that of low-speed nets. The presence of mouth-reduction cones, encasements,

TABLE 6. Formulae for the initial filtration performance of some contemporary plankton samplers with mouth-reducing cones (in terms of the filtration efficiency, F)

Plankton sampler	Towing velocity: 100 cm/sec					Towing velocity which will give an approach velocity of:			
	Filtration efficiency (F)	Mesh velocity (v')	Approach velocity (v)	Dynamic pressure at v cm/sec ($\frac{1}{2} \varrho v^2$)	Filtration pressure ($K \cdot \frac{1}{2} \varrho v^2$)	$v = 5$	$v = 10$	$v = 15$	$v = 20$
		(cm/sec)	(cm/sec)	(g/cm^2)	(g/cm^2)	(cm/sec)			
Large Juday	—	32 F	13 F	0.085 F^2	—	39/F	77/F	116/F	155/F
Hensen Egg	—	48 F	21 F	0.224 F^2	—	24/F	48/F	72/F	95/F
Tropical Juday	—	24 F	7.6 F	0.030 F^2	—	66/F	131/F	197/F	263/F
Kitahara	—	24 F	7.6 F	0.030 F^2	—	66/F	131/F	197/F	263/F
Miller I	—	3.6 F	2.0 F	0.002 F^2	—	246/F	491/F	737/F	982/F
Jet	—	3.7 F	1.8 F	0.002 F^2	—	281/F	563/F	844/F	1125/F
Miller II (coarse)	—	3.8 F	2.0 F	0.002 F^2	—	250/F	500/F	750/F	1000/F
Miller II (medium)	—	4.5 F	2.0 F	0.002 F^2	—	250/F	500/F	750/F	1000/F
Gulf-III modified	—	7.6 F	3.4 F	0.006 F^2	—	149/F	298/F	447/F	595/F
Hardy recorder	—	8.5 F	3.1 F	0.005 F^2	—	159/F	319/F	478/F	638/F
Isaacs high speed	—	8.9 F	2.7 F	0.004 F^2	—	187/F	373/F	560/F	747/F
Bary catcher	—	9.1 F	5.0 F	0.013 F^2	—	100/F	200/F	300/F	400/F
Hardy sampler	—	12.3 F	4.6 F	0.011 F^2	—	109/F	219/F	328/F	438/F
Gulf III	—	31 F	14 F	0.096 F^2	—	36/F	73/F	109/F	145/F
Small Hardy indicator	—	43 F	16 F	0.132 F^2	—	31/F	62/F	93/F	124/F
Standard Hardy indicator	—	71 F	26 F	0.356 F^2	—	19/F	38/F	57/F	76/F

valves, constricted exhausts, or combinations of these, affects flow through these samplers more than does the filtering surface. For example, Bary *et al.* (1958) compared the flow through a 23 cm diameter cylindrical tube with the flow through the body of an encased sampler 23 cm in diameter at the entrance and exhaust and 30 cm in body diameter, the comparison being made both with nets and without. The filtration performance of the sampler, based on the volume of water contained in a 23 cm diameter cylinder projected ahead of the entrance, was 58 per cent for the sampler body without a net, 51 per cent for the sampler with a coarse net, and 46 per cent for the sampler with a fine net. The effective radius of collection corresponded to 11.4 cm for the open cylinder, 8.7 cm for the sampler with a coarse net, and 7.7 cm for the sampler with a fine net.

Because of this dependence upon their shape and their design, we have not attempted to estimate the filtration efficiency of such complex samplers. The comparison of filtration performance given in Table 6 is based upon an unknown filtration efficiency (F) which can be replaced with empirical values as they become available. It is probable, for instance, that the Miller nets, the Jet net, the Hardy recorder, and the modified Gulf III would be found to have relatively low filtration pressures at, say, 6-12 knots, while the Hardy indicators would be found to have relatively high filtration pressures. This conclusion must be weighed against the following observations: the Jet net has been launched and recovered at speeds as high as 18 knots (967 cm/sec) and living crustaceans have been taken from the sample (Clarke, personal communication); Miller high-speed nets are used routinely to 8 knots, but damage to fish larvae occurs at higher speeds (Le Brasseur, personal communication); Ahlstrom (personal communication) noted damage to fish larvae in the modified Gulf III at 9 knots, which was not evident at 6 knots; Glover (1953) found that catches with Hardy indicators 'suffer some squashing', whereas catches taken by the small Hardy sampler were 'quite undamaged'.

A section on terminology, and the bibliography (pages 123-144 of this monograph), follow reprint no. 56, "Field Techniques," by Jack W. Gehringer and William Aron.

ANOMALOUS SIPHONS IN TWO SPECIES OF BIVALVE MOLLUSKS

By HASKELL S. TUBIASH[1], CARL N. SHUSTER, JR.[2]
AND JOHN A. COUCH[1]

This report concerns anomalous siphonal structures of the soft-shell clam, *Mya arenaria,* and the northern quahaug, *Mercenaria mercenaria.* Unusual shell configurations of these two species have been reported (Morse, 1928; Blake, 1929; Fisher, 1932; Parker, 1932; Clench, 1948; and Shuster, 1966). None of these shell malformations appear to be related to the siphonal aberrations considered here and to our knowledge these anomalies have not been described previously. Three specimens formed the basis for this report; specimens 1 and 2 were soft-shell clams and specimen 3 was a quahaug.

Specimen 1 (Page 120, fig. 1) was discovered among a group of clams collected in Chesapeake Bay and maintained at the Oxford Biological Laboratory for experimental use. Except for the supernumerary portion of the incurrent siphon, specimen 1 appeared normal in all respects. The tip of the supernumerary process was clearly apparent, even when the siphons were fully retracted (fig. 1a). When the siphons were extended, this process projected about midway along the ventral aspect. In the living, relaxed animal, the anomalous process was about 12 mm. long and had proximal and distal diameters of approximately 7 and 5 mm., respectively (fig. 1b). This supernumerary process could contract and expand, but not as much as the primary siphons. Terminal tentacles similar to those surrounding the lumina of normal siphons were absent.

The accessory siphon was dissected along its longitudinal axis and across the axis of the normal siphons. The interior of the accessory process was a short blind sac anastomosed to the adjacent incurrent siphon, but the lumen did not extend to the distal end. Histological examination revealed a predominance of longitudinal muscle fibers at the proximal end of the process, and a mixture of circular and longitudinal fibers at the distal

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[1] Biological Laboratory, U. S. Bureau of Commercial Fisheries, Oxford, Maryland 21654.

[2] Northeast Marine Health Sciences Laboratory, USDHEW, PHS, Narragansett, Rhode Island 02882. Contribution no. 27.

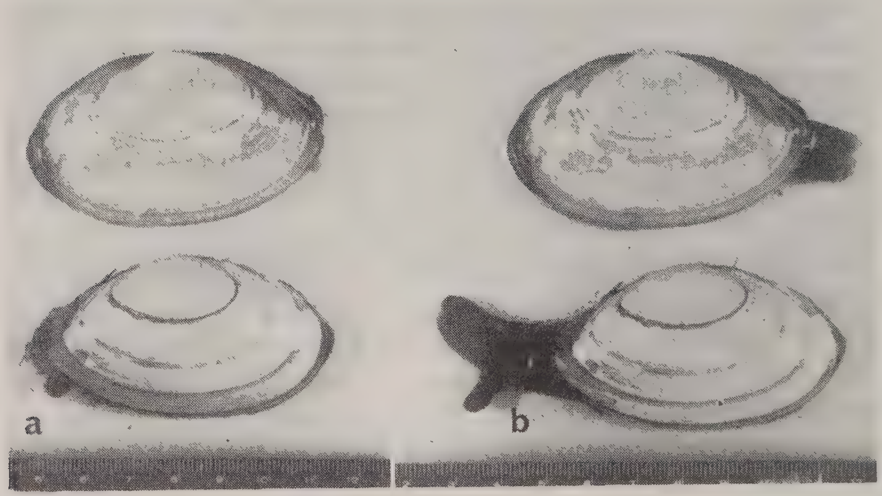

Figure 1. Soft-shell clam with a nonfunctional supernumerary appendage on the incurrent siphon: a) siphons retracted, normal clam above and clam with anomalous siphonal condition below; b) same specimens, showing semi-extended siphons and the lack of tentacles on the distal end of the appendage.

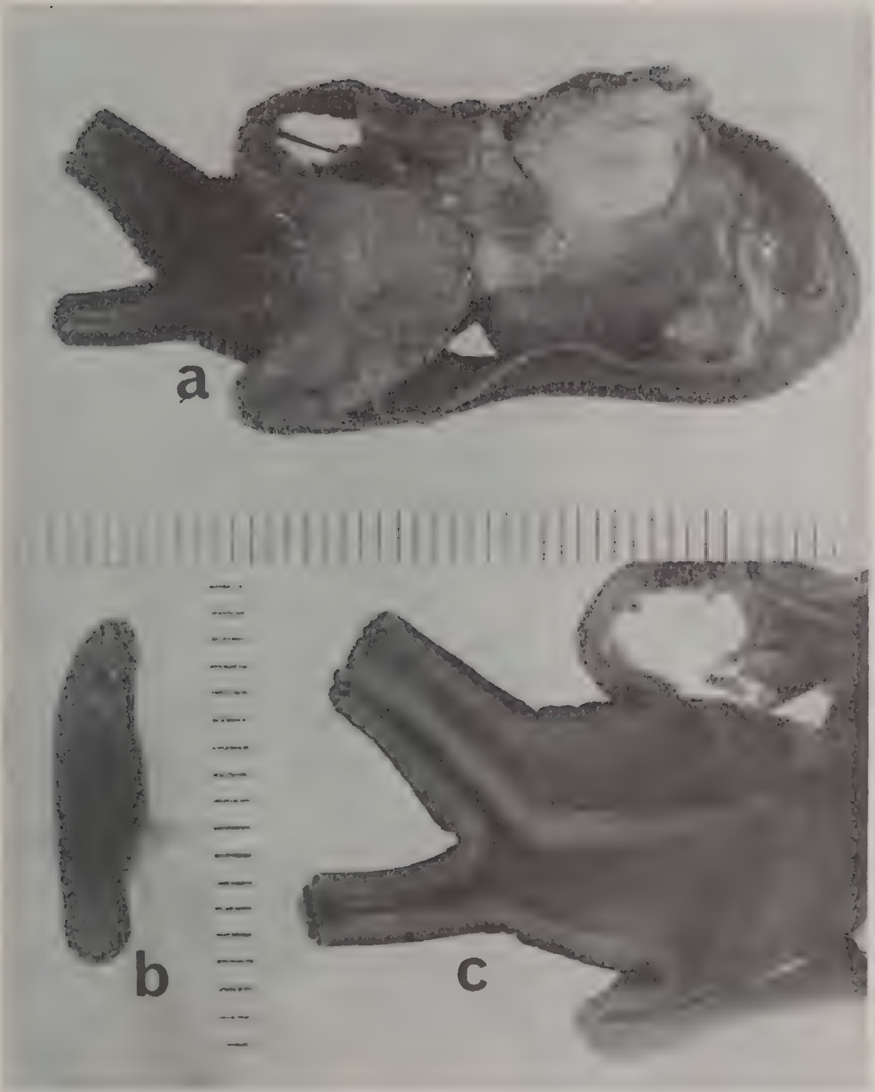

Figure 2. Soft-shell clam with a bifurcated incurrent siphon: a) the shucked, preserved specimen; b) view of the distal portions of the siphons; and c) a freehand sagittal section showing the pigmentation and the continuity of the siphonal lumina. The three illustrations are oriented in relation to each other; the scale is in millimeters.

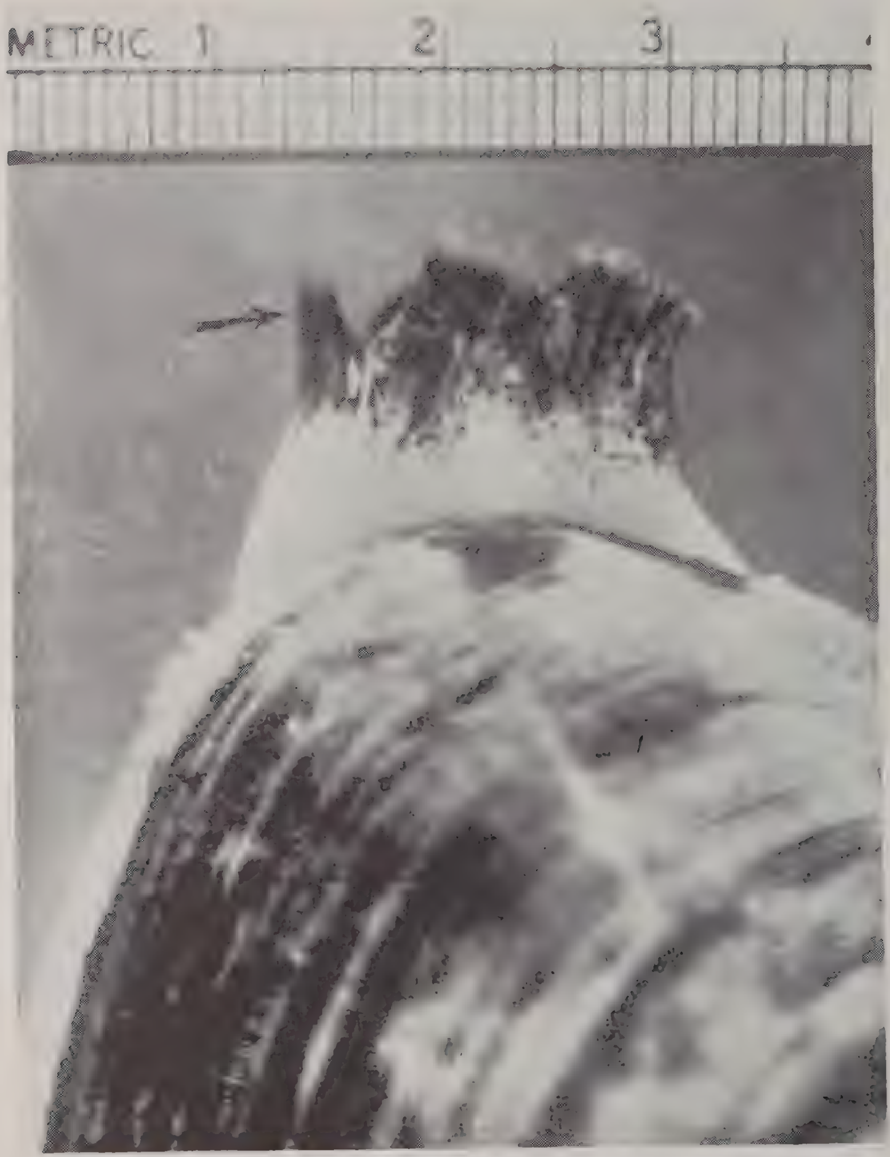

Figure 3. Northern quahaug with a nonfunctional supernumerary appendage (arrow) on the incurrent siphon; tentacles are apparent on the appendage.

end. There was no evidence of previous injury, of active cellular proliferation, or of neoplastic activity to account for the anomaly.

Specimen 2 (fig. 2a) was collected in New Hampshire and donated to the Northeast Marine Health Sciences Laboratory. It was received shucked and preserved in rubbing alcohol. This specimen had 3 normal-appearing siphonal orifices with surrounding tentacles (fig. 2b). A freehand sagittal section of the siphons showed that the incurrent siphon was bifurcate with connecting lumina and normal pigmentation (fig. 2c).

Specimen 3 was discovered among locally harvested quahaugs at the Northeast Marine Health Sciences Laboratory, where staff members observed its siphonal activity. The incurrent siphon (fig. 3) had a supernumerary structure on the ventral wall. This anemone-like projection terminated in a distal whorl of tentacles, not unlike normal siphons, but a functional opening seemed to be lacking. Several observations, with and without the use of dyes, failed to demonstrate passage of water into or out of the projection, whereas the normal portion of the siphons showed the usual water circulation. Pigmentation of the projection was continuous with that of the incurrent siphon. Activity of the siphons, particularly during extension and retraction, indicated that the musculature of the accessory projection was closely associated with that of the siphon proper. The specimen died and decomposed before additional information could be obtained.

These three examples show that similar siphonal anomalies may occur among two nonrelated species of bivalve mollusks. The causes of the anomalies are unknown to us, but they may be the result of genetic or developmental aberrations or predator injury. Crabs and fish are known to prey on siphon ends of clams (Morse, 1919; Turner, Ayers and Wheeler, 1948; Medcof and MacPhail, 1952), but *Mya* can survive siphonal injury and often regenerates normal tentacles (Belding, 1930; Medcof and MacPhail, 1952). Whether an incision or the loss of a small portion of siphonal tissue could lead to the formation of a supernumerary siphon or accessory process is a matter of speculation.

Acknowledgements. We thank Judith Young, Dover, New Hampshire, for donating Specimen 2. Paul W. Heffernan discovered Specimen 3 and Frances C. Garb assisted in observations of its siphonal activity.

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The Skipjack Tuna Fishery in Palau

by

Richard N. UCHIDA
Bureau of Commercial Fisheries Biological Laboratory
Honolulu

Skipjack tuna (Katsuwonus pelamis) fishing in Palau has a history going back to the decade prior to the outbreak of World War II. From fishing bases established in Palau, Truk, Ponape, and Saipan in the former mandated islands, Japan carried on both longline fishing for large, subsurface tunas and billfishes, and pole-and-line fishing for surface schools of skipjack tuna. The Japanese stopped fishing these waters at the outbreak of war.

The present fishery for skipjack tuna is conducted by live-bait boats contracted to an American firm operating a freezer-storage plant in Palau. The boats are manned by Okinawan fishermen as well as Micronesian trainee-fishermen.

Historical data on catch and fishing effort and more recent data on skipjack tuna sizes and sexual maturity permit description of the fishery.

The principal baitfish is the anchovy, Stolephorus heterolobus, which are captured at night with the aid of a light to attract the fish. On the fishing grounds, schools are located by scouting for birds which are usually associated with the fish. Scouting is discontinued as darkness approaches and the vessels usually head for port to unload the day's catch.

In 1936, the Japanese had between 9 and 32 vessels fishing each month. Monthly catches ranged from 8.7 metric tons in February to 770.4 metric tons in December. The number of fishing trips ranged from 26 in February, to as many as 612 in June. Catch per trip varied from 0.3 metric ton in February to 1.4 metric tons in November.

The average size of the skipjack tuna varied from month to month between 36 and 52 cm in 1936; in 1965-67, they ranged between 48 and 62 cm. For all years in which size data were examined, there was a pronounced tendency for the average size to increase in October-January. This increase in average size corresponds roughly to the increase in catch per trip in winter.

Reprinted from Report of the Symposium on the Cooperative Study of the Kuroshio and Adjacent Regions (CSK), Report and Abstracts of Papers, FAO Fisheries Report No. 63, p. 53, 1968.

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SULFONAMIDE INHIBITION IN *MONOCHRYSIS LUTHERI*[1]

Ravenna Ukeles
U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Biological Laboratory, Milford, Connecticut 06460

SUMMARY

The effect of sulfonamides on growth of the chrysomonad, Monochrysis lutheri, *in a synthetic seawater medium was examined over a period of 14 days. The population increased at all sulfonamide concentrations during the first several days of incubation before inhibition became apparent. Inhibitory concentrations ranged from 0.01 to 1.0 mg%. Inhibition was most pronounced in sulfathiazole; sulfamethazine, sulfapyridine, and sulfanilamide followed in decreasing order. p-Aminobenzoic acid (0.001–1.0 mg%) competitively reversed inhibition. Folic acid, thymine, adenine, and vitamin B_{12} neither reversed the inhibition nor spared the requirement for p-aminobenzoic acid. The significance of the inhibition pattern and the potential use of antimetabolites in the marine environment were discussed.*

INTRODUCTION

Antimetabolites have been intensely studied in various biological systems (*16,31*), but little is known of their effects on unicellular algae, particularly marine species. Johnston (*17*) has suggested that difficulties in studying phytoplankton nutrition, whenever species cannot be maintained on a synthetic medium, could be overcome by applying "inhibition analysis," as described by Shive (*28*). Information on the extent of inhibition of a given species in a synthetic medium by a particular antimetabolite could be applied to assay the metabolite in the environment. A connection may exist between susceptibility to antimetabolites and phytoplankton succession in the marine environment (*17*).

Sulfonamides have been among the most frequently investigated antimetabolites. Reports on effects in unicellular algae, however, have been sporadic, often not in well-defined systems, and limited to a few types. Early studies were with freshwater chlorophytes (*4,7*) and diatoms (*29*). Lewin (*21*) observed growth inhibition of *Chlamydomonas moewusii* in sulfanilamide; a similar effect in *Scenedesmus obliquus* was reported (*19*). Perlman (*26*), working with *Chlorella pyrenoidosa* and *S. obliquus*, concluded that algae do not resemble bacteria in their response to sulfonamides. Effects of sulfanilamide and the development of resistant strains in the colorless flagellates, *Polytomella caeca* and *Chilomonas paramecium*, were studied extensively by Lwoff *et al.* (*22*) and Hall (*13,14*). Johnston (*17*) reported on the sensitivities to sulfanilamide of bacterized and bacteria-free strains of marine algae that included diatoms, dinoflagellates, and chlorophytes. We observed that growth of the marine chrysophyte, *Monochrysis lutheri*, was inhibited in low concentrations of sulfamethazine. In the present study, the effects of related sulfonamides on growth were investigated.

MATERIALS AND METHODS

An axenic strain of *M. lutheri* maintained in our laboratory for several years on the artificial seawater medium, ASP_2 (*27*), was used. The basal medium for experiments consisted of ASP_2, modified by the omission of folic acid, *p*-aminobenzoic acid (PABA), thymine, and vitamin B_{12}. Stock solutions of sulfamethazine, sulfapyridine, sulfathiazole, and sulfanilamide were each prepared in alkaline distilled water. The pH of the final growth medium was adjusted to 8.2 before sterilization. Aliquots of 9 ml were dispensed into optically matched 20 × 150 mm Pyrex test tubes with screw caps, and sterilized for 20 min at 15 lb. Since autoclaving solutions of folic acid may decrease activity (*11*), growth factor supplements, such as PABA, thymine, folic acid, and B_{12}, were prepared in modified ASP_2, sterilized with a GS Millipore®[2] filter, and added aseptically to tubes of autoclaved media. Tubes were inoculated with 0.5 ml (5×10^6 cells/ml) of *M. lutheri* from the log phase and incubated under cool white fluorescent lights on a 12-hr light-dark cycle at 20 C. The initial pH of cultures determined after inoculation was 8.0–8.3. The growth response over 14 days was observed by taking daily optical density readings in a Bausch & Lomb "Spectronic 20" colorimeter at 520 mμ. Chemical determinations of sulfonamides were adapted from the method of Bratton & Marshall (*5*).

RESULTS

Inhibition. Figure 1 shows that sulfanilamide had no effect on growth up to the 6th day, except for slight stimulation in the two highest concentrations. A marked divergence in response to different concentrations then took place. In 0.01, 0.05, and 0.1 mg% the effect on the growth curve was small and populations continued to increase at a slightly slower rate than the controls, but after the initial increase in 0.5 and 1.0 mg% a short, stationary phase was followed by a decline in density. Sulfapyridine was more inhibitory than the preceding sulfonamide (Fig. 2). Only in 0.01 mg% did populations continue to increase and reach almost the same densities as the control. Populations in 0.05 and 0.1 mg% did not increase beyond the 7th day and, although in 0.05 mg% growth remained at this density for a pro-

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[1] *Received June 17, 1968; revised August 2, 1968.*

[2] Trade names referred to in this publication do not imply endorsement of commercial products by the Bureau of Commercial Fisheries.

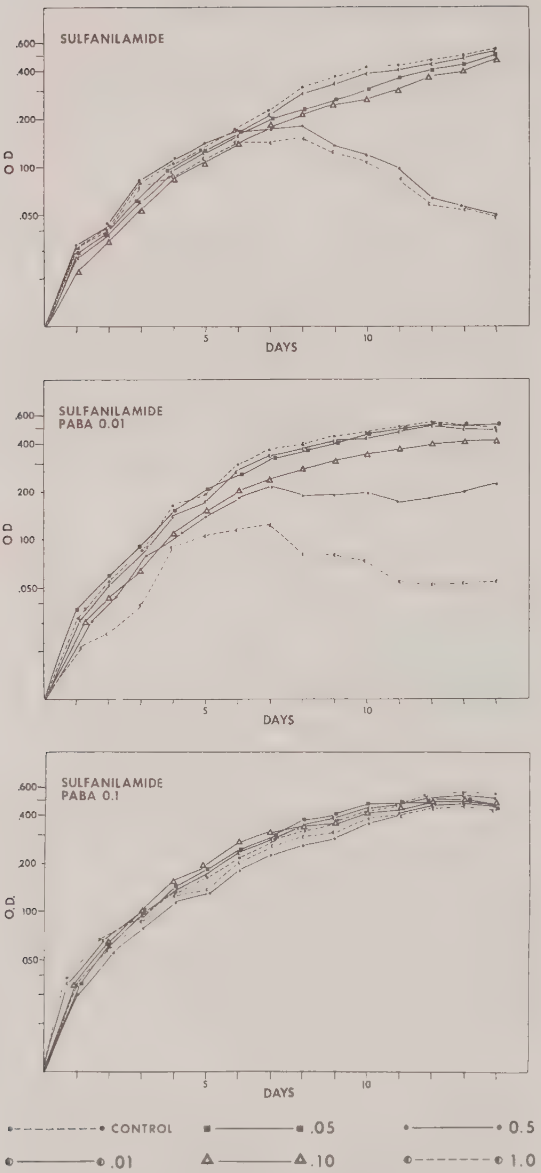

FIG. 1. Growth of *M. lutheri* in sulfanilamide (0, 0.01, 0.05, 0.1, 0.5, and 1.0 mg%), and in sulfanilamide with *p*-aminobenzoic acid (PABA 0.01 and 0.1 mg%).

TABLE 1. *Uptake of sulfonamides during growth.*

Initial concentration (mg%)	Sulfanilamide	Sulfapyridine	Sulfamethazine	Sulfathiazole
	(mg%)			
1.0	0.54	0.53	0.30	0.25
0.5	0.29	0.27	0.12	0.13
0.1	0.07	0.06	0.03	0.03
0.05	0.04	0.03	0.02	0.01
0.01	0.007	0.006	0.001	0.003

longed period, in 0.1 mg% it diminished. In 0.5 and 1.0 mg%, densities began to decrease slowly on the 5th day until cells completely settled out by the 11th. Sulfamethazine and sulfathiazole were generally similar in growth inhibition, the latter being the more effective inhibitor (Fig. 3, 4). In all concentrations the population increased at about the same rate as the control in the first few days, and in 0.01 mg% it continued to do so in both compounds. In sulfamethazine this initial increase was followed by a slow decline in the population in 0.05 and 0.1 mg% and an even more rapid drop in 0.5 and 1.0 mg%. In sulfathiazole the growth rate decreased and the population fell rapidly in 0.05, 0.1, 0.5, and 1.0 mg%.

Sulfonamide uptake. Sulfonamide remaining in the medium after growth was determined ~ 8 days after the cessation of density readings. Suspended cells were sedimented by centrifugation and the medium was analyzed for sulfonamides (Table 1).

Inhibition reversal. Reversal of sulfonamide inhibition was brought about by PABA, 0.01–1.0 mg%. Lower concentrations of PABA (0.001 mg%) counteracted inhibition only in the lowest concentrations of sulfonamide. In a concentration of 0.001 mg% PABA the growth rate in 0.05 and 0.1 mg% sulfanilamide was increased, and in sulfapyridine, sulfamethazine, and sulfathiazole inhibition was partially reversed at 0.05 mg%. Effects of higher concentrations of PABA (10 mg%) were always similar to that of 1.0 mg%, i.e., there was no stimulation or inhibition of growth.

The extent of reversal by 0.01–1.0 mg% PABA depended on the particular sulfonamide. In the two highest concentrations of sulfanilamide, inhibition was partially reversed with 0.01 mg% PABA so that moderate population levels were maintained over an extended period. Increasing PABA to 0.1 mg% completely counteracted the inhibition (Fig. 1). At 0.01 mg%, PABA produced little reversal in 0.5 and 1.0 mg% sulfapyridine, but the decline in growth was prolonged from 5 to 11 days, and the effects of less sulfapyridine were almost completely nullified. Increasing PABA to 0.1 mg% permitted growth almost equal to that in the control, in 0.5 and 1.0 mg%, and the population level was maintained. At 1.0 mg% PABA all sulfapyridine inhibition was reversed (Fig. 2). The inhibitions in 0.05 mg% sulfamethazine and sulfathiazole were reversed with 0.01 mg% PABA. Effects of 0.1 mg% were partially counteracted, but the two highest concentrations were not influenced. With 0.1 mg% PABA, inhibition was almost completely reversed in all concentrations of sulfamethazine, but not in 1.0 or 0.5 mg% sulfathiazole. Growth inhibition in all concentrations of sulfamethazine and sulfathiazole was abolished in 1.0 mg% PABA.

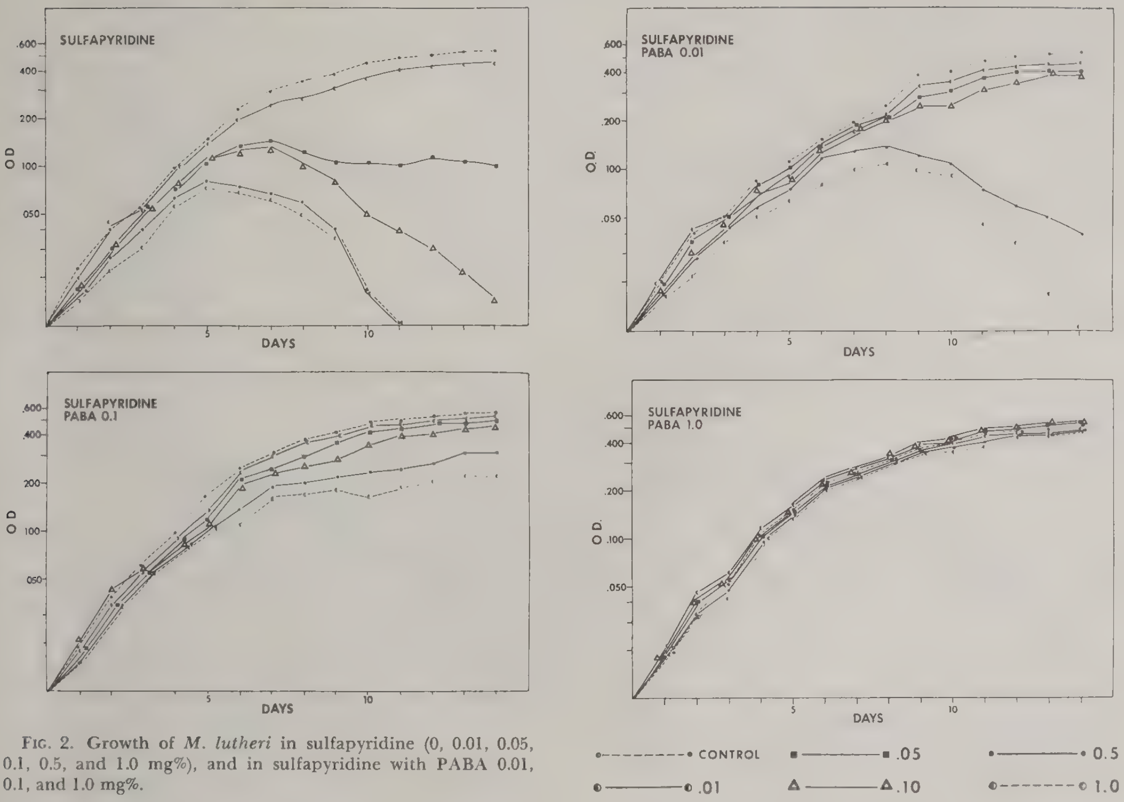

FIG. 2. Growth of *M. lutheri* in sulfapyridine (0, 0.01, 0.05, 0.1, 0.5, and 1.0 mg%), and in sulfapyridine with PABA 0.01, 0.1, and 1.0 mg%.

Other compounds were also tested for inhibition reversal, but found to be without effect. The potential reversing agents by themselves were neither stimulatory nor inhibitory in a wide concentration range, e.g., folic acid, 0.5–1.5 mg%; thymine, 0.5–5.0 mg%; methionine, 0.5–10 mg%; and PABA, 0.0001–20 mg%. Folic acid (0.05–1.0 mg%) had no effect on growth inhibition in sulfanilamide (0.5, 1.0 mg%). Also, it did not spare PABA (0.001, 0.01 mg%) requirements needed for reversal. Sulfanilamide inhibition was also not reversed by vitamin B_{12} (0.5–5.0 μg%) nor did it spare PABA requirements for reversal. Also, thymine (0.5–5.0 mg%) was without effect on reversing inhibition of sulfamethazine, sulfapyridine, or sulfathiazole (0.1–0.05 mg%). A mixture of vitamin B_{12} (0.2 μg%), thymine (0.3 μg%), PABA (1.0 μg%), and folic acid (0.2 μg%) also did not affect the sulfonamide inhibition.

DISCUSSION

The close similarity in structure, size, and bond angles (*3*) between the *p*-aminobenzoate and sulfanilamide ions provided a physical basis to support the theory of sulfanilamide competition with PABA. Most of the other sulfonamides are derived from sulfanilamide by the introduction of heterocyclic radicals to the amide group (Fig. 5), which has the effect of enhancing or diminishing the toxicity of sulfanilamide. The relative inhibitory activity of the sulfonamides in *M. lutheri* was similar to that reported for many bacteria (*3*), but the reverse of that in diatoms (*29*). In *M. lutheri*, inhibition was correlated with sulfonamide acid dissociation constants. The stronger the acid, the more effective was inhibition. The most inhibitory sulfonamide was sulfathiazole pK_a 7.12, and in decreasing order of activity were sulfamethazine, pK_a 7.37; sulfapyridine, pK_a 8.43; and sulfanilamide, pK_a 10.43. The relative inhibition produced by the different sulfonamides and the data on sulfonamide uptake suggest that the neutral molecule penetrates the cell but inhibitory activity is carried out by the ion. Although less sulfathiazole is in molecular form and less penetrates the cell in this medium than with other sulfonamides, it was the strongest inhibitor. The sulfonamides belong to a group of substances whose biological activity is increased by decreasing the ionization on the outside of the cell membrane, but whose action on the inside of the membrane takes place as the ion (*1*). PABA with pK_a 4.8 exists largely in the anionic form in this growth medium and probably very little penetrates the flagellate. Lwoff *et al.* (*22*)

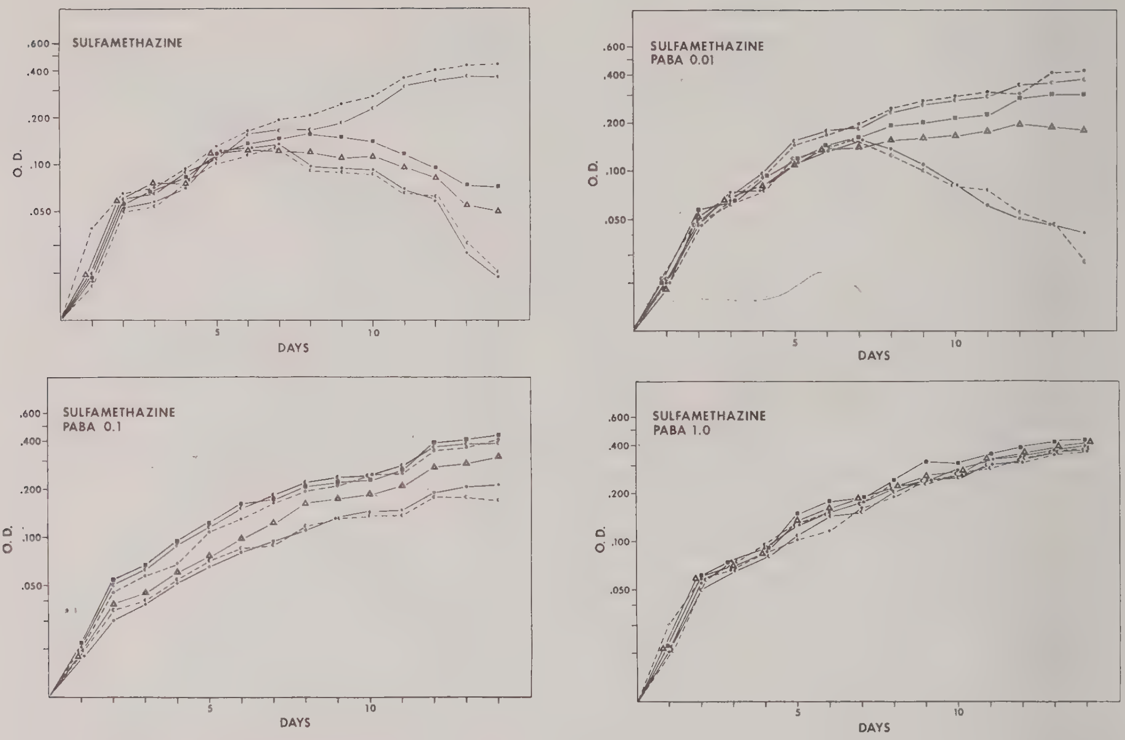

Fig. 3. Growth of *M. lutheri* in sulfamethazine (0, 0.01, 0.05, 0.1, 0.5, and 1.0 mg%), and in sulfamethazine with PABA 0.01, 0.1, and 1.0 mg%.

found that the activity of PABA was pH dependent: maximum activity or uptake occurred at minimum dissociation.

The competitive reversal of inhibition by PABA depended on the potency of the antimetabolite, i.e., higher concentrations were required in the more active sulfonamides. The inhibition index (ratio of sulfonamide to PABA at which effects are counterbalanced) would probably increase from the low values found in this growth medium if the organism could be cultured in a more acid medium. With sulfanilamide the inhibition index was 50–100, but with other sulfonamides it was 1–10. Comparisons between species are not valid because the index depends, to a large extent, on the pH of the growth medium and the criterion used to judge inhibition reversal. Other studies in which the growth medium was in the acid range reported inhibition indexes 10- to 100-fold greater (*13,26*) than with *M. lutheri*. Inhibition sometimes refers to a reduction in growth rate, and at times to a culture having a smaller viable count than a control at some arbitrary time after inoculation. Without information on the actual appearance of the growth curve and a description of conditions of incubation, however, values on the index alone are not useful. The observations of Moore & Boylen (*25*) emphasized the importance of studying growth rates over a period of time, especially in inhibition studies. *M. lutheri* cultures initially gave an almost normal response in the presence of the sulfonamides, and the degree of inhibition became apparent only after an extended incubation period. A different type of growth response was reported for other flagellates (*13,22*). In some strains, after an extended period of slow growth, the curve changed and rapid growth was resumed. Blondel (*4*) described 2 types of response to sulfanilamide by nonmotile chlorophytes. One had a lengthy period of poor growth. In the other this was overcome and growth continued at a normal rate. This type of spontaneous reversal of inhibition and the development of resistant strains were not observed in *M. lutheri*. It appears as if this flagellate has reserve pools of metabolites essential to cell division which must become depleted before the effect of the sulfonamide on growth becomes apparent. The growth curve can be understood by examining the role of PABA in metabolism.

Early work suggested that the utilization of PABA was blocked by sulfanilamide (*30*), and that in some

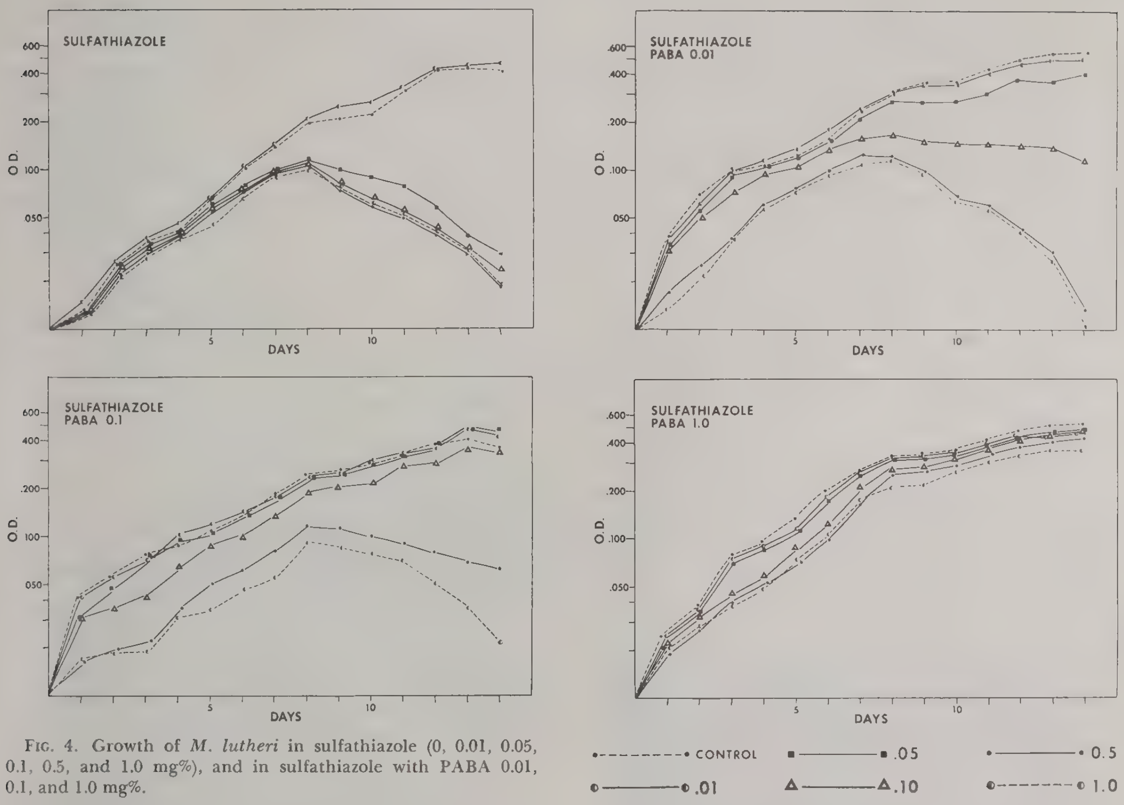

FIG. 4. Growth of *M. lutheri* in sulfathiazole (0, 0.01, 0.05, 0.1, 0.5, and 1.0 mg%), and in sulfathiazole with PABA 0.01, 0.1, and 1.0 mg%.

way this interfered with the synthesis of folic acid (*23,24*). The role of PABA became clear when it was shown to be an essential part of the folic acid molecule (*2*). In cell-free extracts of *Escherichia coli*, sulfonamides specifically inhibit the enzymatic reaction where dihydropteroic acid is formed from PABA and dihydropteridine in the presence of ATP and Mg^{++} (*6*). The suggestion has been made that sulfonamide-sensitive microorganisms not utilizing folic acid for reversal are unable to bypass the inhibited biosynthetic reactions by utilization of exogenous folic acid because they lack folic reductase, as distinct from dihydrofolic reductase (*18*). Folic acid, as such, is metabolically inactive (*15*) and must be converted to the active form, dihydrofolic acid, before the coenzyme derivatives can be formed. Since folic acid coenzymes play an essential role in the formation of thymine, adenine, and guanine, prevention of folic acid synthesis can be expected to interfere with cell division after DNA reserves are depleted. In *M. lutheri* the extended period of normal growth before inhibition occurs seems to indicate large amounts of DNA in this flagellate.

Certain microorganisms require the complete folic acid molecule, e.g., the protozoan, *Tetrahymena geleii* W (*20*), and the bacterium, *Lactobacillus casei* (*12*), therefore, they are actually insensitive to sulfonamides. Inhibition in *M. lutheri* constitutes indirect evidence that enzymes active in the synthesis of folic acid are present. Noncompetitive reversal of inhibition by structurally unrelated metabolites whose synthesis is folic catalyzed, such as methionine, serine, thymine, and purines, has been reported in many bacterial systems. Vitamin B_{12} also reduces the requirements for PABA in reversal of sulfonamide inhibition (*28*). Although PABA demonstrated competitive reversal of inhibition in *M. lutheri*, there was no hint of reversal with these structurally unrelated agents.

Inactivity of folic acid or folic-catalyzed products in reversing inhibition may be due to an inability to absorb such products or to lack of enzymes converting the reversing agent to the active form. There is no reason, a priori, for accepting the first hypothesis, particularly as there is evidence that *M. lutheri* is permeable to vitamin B_{12} and its analogs (*8,10*). Since folic acid has multiple roles in synthesis, it is possible that supplying the end product of only one of these reactions is insufficient to suppress inhibition. More likely, activation mechanisms for the utilization of these metabolites are absent. In this regard it is interesting that methionine and

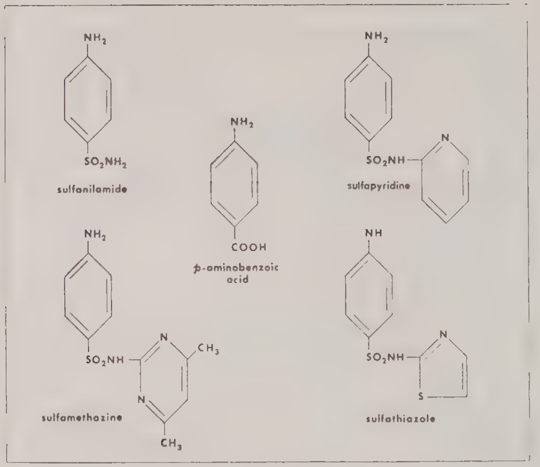

FIG. 5. Structures of sulfonamides and PABA.

serine were not utilized by *M. lutheri* in growth experiments (*9*).

Antimetabolites, very useful in studies of plant and animal nutrition and in biochemical processes, could similarly be applied to phytoplankton investigations. The natural environment could be assayed for the presence of organic metabolites after metabolite-antimetabolite relationships are characterized under controlled conditions. Although inhibition reversal in natural seawater can only give presumptive evidence for the presence of metabolites, since reversal is not a definitive test for a structural analog, it does afford a simple and sometimes highly sensitive test for metabolites. Interpretation of results may then be confirmed with independent evidence from other techniques.

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A Mycosis of the Gills of the Pandalid Shrimp, *Dichelopandalus leptocerus*

JOSEPH R. UZMANN

U.S. Bureau of Commercial Fisheries Biological Laboratory,
West Boothbay Harbor, Maine 04575

AND

EVAN B. HAYNES[1]

U.S. Bureau of Commercial Fisheries Biological Laboratory,
Woods Hole, Mass. 02543

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A fungus disease of the pandalid shrimp, *Dichelopandalus leptocerus,* is described and a partial life cycle is proposed. The causal agent is a chytridlike phycomycete. Infection is limited to the branchial lamellae in which thallus development causes necrosis of the lamellar tissue matrix.

This report describes a chytridlike parasite of the gills of *Dichelopandalus leptocerus* and illustrates the stages of its life cycle that can be deduced from available samples.

The disease was initially observed by one of us (E.B.H.) in formalin-preserved collections of *D. leptocerus* from trawl surveys of the New England continental shelf by the R/V *Albatross IV* in June 1963, January 1964, and October 1966. Infection rates in these samples were 121 of 233 (52%), 278 of 517 (54%), and 570 of 591 (96%), respectively. Diseased shrimp occurred at 79 of 126 (63%) sampling locations ranging from southern Nova Scotia to the continental slope off southeastern Long Island, New York.

Development of the parasite is confined to the branchial lamellae of the host shrimp. Detection of light infections requires removal of the overlying carapace and direct

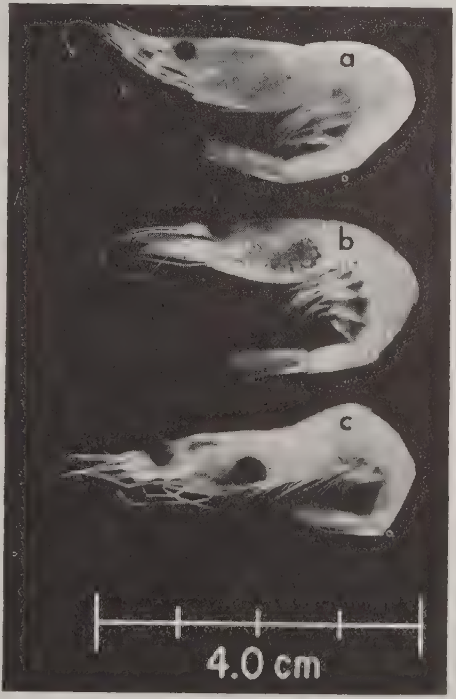

FIG. 1. Gross appearance of mycotic gill disease in *Dichelopandalus leptocerus:* (a) light infection; (b) moderate infection; (c) advanced infection.

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[1] Present address: U.S. Bureau of Commercial Fisheries, Biological Laboratory, Auke Bay, Alaska 99821.

examination of the lamellae. More acute infections are indicated by grossly visible mottling or darkening of the collective lamellae that may be seen even before removal of the carapace; the discoloration is a result of necrotic zonation about sites of infection. In severe cases, the entire branchial apparatus may appear black or dark brown (Fig. 1).

A partial life cycle is suggested in Plate I, Figs. 2–11. The drawings are based on

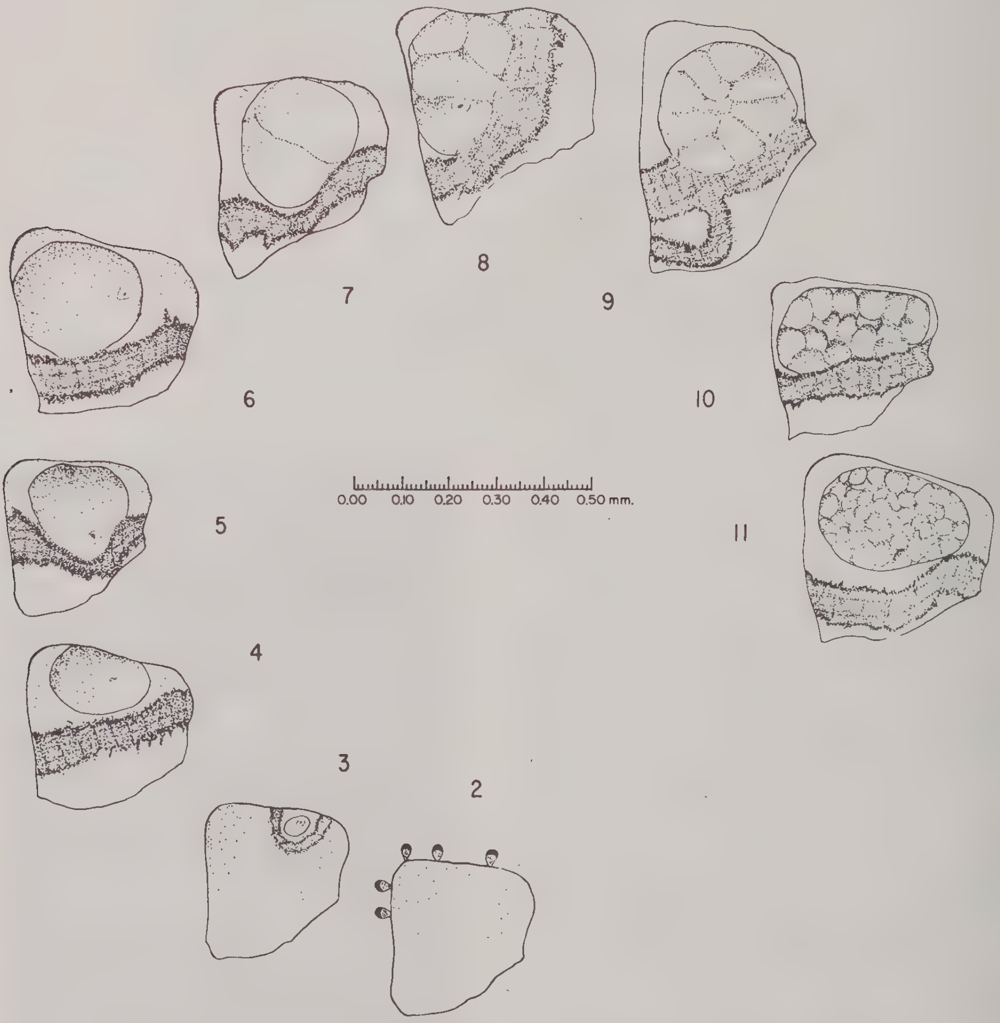

PLATE I

Plate 1, Figs. 2–11. All figures from camera lucida outline drawings with freehand detail. 2. Lamella with attached zoospores along free margin. 3. Lamella containing early-stage thallus with concentric zone of necrosis. 4. Lamella containing midstage thallus; in this and succeeding stages, distal portion of lamella is blisterlike, hollow, and partitioned from medial portion by a transverse zone of necrotic tissue. 5. Advanced stage thallus. 6. Mature thallus beginning to cleave. 7. Thallus becomes walled, first cleavage complete, transition into sporangium. 8. Sporangium with 4 cells. 9. Sporangium with 8 cells. 10. Sporangium with 17 cells. 11. Sporangium with 45 cells.

microscopical study of stained whole mounts and histological sections of selected lamellae from six heavily infected specimens collected at Veatch Canyon (40°05′N., 69°35′W.) in October 1966. Fully matured sporangia were not evident in any of the Veatch Canyon specimens, nor in heavily infected specimens from 11 other sampling localities; we are unable, therefore, to postulate morphological development beyond that indicated in Fig. 11.

Diagnosis. Thallus holocarpic, monocentric, endobiotic, intramatrical; early thallus spherical, becoming lenticulate at maturity in order of 350 μ diameter; thallus initially naked, later becoming walled, lacking visible rhizomycelium; mature thallus transforms directly into a sporangium by repeated bipartitions of protoplast to produce an underdetermined number of spores in excess of 32. Bipartitions of protoplast usually synchronous through 8-cell stage, at least. Settled zoospores (possibly zygospores) obovate, about 30 μ long with deeply staining polar cap; commonly attached to free margins of lamellae.

Remarks. The organism is tentatively placed in the Class Phycomycetes on the basis of the above-described characteristics and the assumption of production of motile spores; further nomenclatural assignments must await observation of spore flagellation.

The gross and microscopic pathology of this disease suggests that it must have serious effects on the respiratory efficiency of the host. The high incidence of the disease in all parts of its observed range further suggests that it may be an important cause of natural mortality in *D. leptocerus* populations and perhaps of other potential hosts as well. Failure to find fully matured sporangia in large series of samples from a wide range in space and time may indicate that terminal stages of parasite development and liberation of zoospores occur at death of host, or at some stage of morbidity that limits the host's swimming ability above the substrate and hence availability to capture in trawls.

ACKNOWLEDGMENT

We thank Dr. Roland L. Wigley of the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, who kindly made available the extensive series of samples from which this study was made.

Early Larvae of the Canary Rockfish, *Sebastodes pinniger*

Rockfishes of the genus *Sebastodes* are ovoviviparous or oviparous (if oviparous, the young are hatched immediately after the ova are extruded from the female). Pigment patterns on advanced embryos or early larvae from a gravid female rockfish of known identity aid in identifying more advanced larvae. Using this approach, Morris (1956) and Delacy et al. (1964) described early larvae of 13 species of *Sebastodes* from the eastern Pacific Ocean. This note presents the first description of early larvae of the canary rockfish, *Sebastodes pinniger* (Jordan and Gilbert), 1880.

A 57-cm gravid female canary rockfish was caught in a Cobb pelagic trawl on January 12, 1965, off the Washington coast at 47°47′N lat, 124°52′W long. Eggs containing advanced embryos were oozing from the fish; some of them were collected and placed in a container of sea water. At the laboratory 2 days later, 75 eggs were transferred to petri dishes containing sea water (salinity 32‰, temperature 10 C); the rest were preserved in formalin. Most of the live embryos were still in the eggs, but a few had hatched, possibly as a result of handling. The ellipsoidal preserved ova had average measurements of 1.45, 1.23, and 0.84 mm. In dorsal aspect 145 embryos curved to the left, and 130 curved to the right within the eggs.

All of the live embryos had hatched by January 15; the larvae remained on the bottom of the petri dishes and moved only occasionally. On January 21 the jaws moved but not the eyes. By January 22 the larvae had become fairly active and could maintain position in mid water for some time. In the shallow dishes in which they were kept, however, they soon sank to the bottom. No attempt was made to feed the larvae and except for a few that died from natural causes, all were killed and preserved by February 1.

The yolk sacs had decreased in size but were still present in the larvae preserved on February 1. The standard length had changed little. The average for 23 larvae preserved on January 14 was 3.6 mm (3.1–3.9 mm); the average for 6 larvae preserved on January 29 was 3.8 mm. Pectoral fin length increased from about 0.1 mm on January 14 to about 0.5 mm on January 29.

The amount of pigment on the larvae gradually increased during the 2-week period after hatching. Until January 18, the only melanophores were an irregular double row along the ventral body surface from the 18th to 22nd myomeres and a small patch above the yolk sac near the anus (Fig. 1). Larvae preserved on January 18 and 19 showed one or two melanophores along each side above the ventral row, apparently migrating dorsally. These lateral melanophores were lacking on larvae preserved at later dates. By January 22 a short, irregular double row of melanophores was present along the dorsal body surface on the 19th–21st myomeres, and single melanophores were

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visible at the tip of the lower jaw and in the hypural region. After January 26 one to four melanophores were present on the ventral part of the yolk sac; by February 1 the pectoral fins carried several small melanophores.

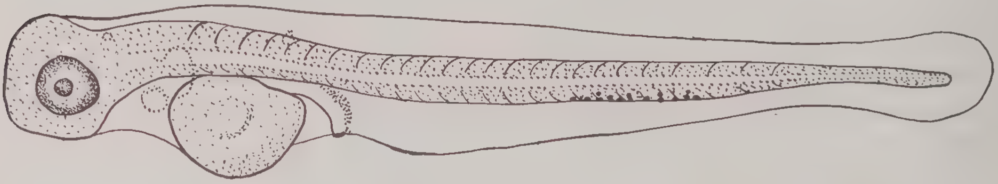

FIG. 1. Pigment pattern of newly hatched canary rockfish.

Length of the ventral pigment row varied on larvae preserved from January 28 to February 1; the most anterior melanophores were on myomere 14–18 and the most posterior on myomere 21 or 22.

Immediately after hatching, the larvae resembled those of *S. paucispinis* as described by Morris (1956). After 2 weeks of development, and an increase in the pigment, larvae of *S. pinniger* (Fig. 2) resembled newly hatched *S. jordani* of Morris (1956), although *S. pinniger* had shorter dorsal and ventral rows of melanophores.

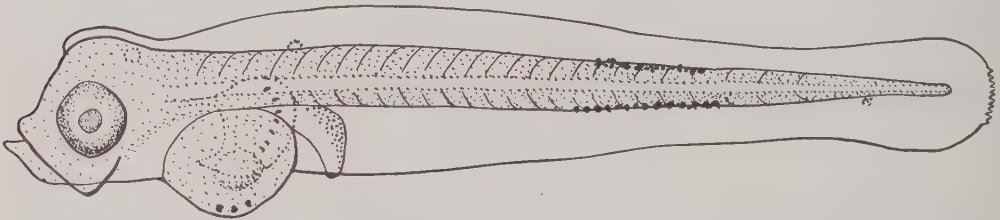

FIG. 2. Pigment pattern of canary rockfish 2 weeks after hatching.

A number of small serrations had developed along the posterior edge of the caudal finfold of specimens preserved on and after January 26; these serrations could be seen on anesthetized, living specimens and thus cannot be considered an artifact of preservation.

Morris (1956) mentioned a "small discoidal indentation" on the dorsal finfold of his specimens. Two pairs of such structures were observed on *S. pinniger* — one pair on the dorso-lateral body surface at about the fifth myomere and the other just behind and slightly above the eyes.

The features considered by Morris (1956) and Delacy et al. (1964) in their descriptions of other *Sebastodes* larvae are presented below for *S. pinniger.* The measurements given are averages of 10 specimens of newly hatched larvae; the pigment patterns are for newly hatched and 2-week-old larvae.

Measurements of newly hatched larvae: standard length, 3.61 mm; diameter of eye, 0.27 mm; tip of snout to anus, 1.24 mm; tip of snout to posterior edge of otic capsule, 0.51 mm; body depth in region of heart, 0.53 mm.

Larval Pigment Patterns

	Newly hatched larvae	2-week-old larvae
Ventral pigment row present	+	+
Ventral pigment row stops short of anus	+	+
Ventral pigment row multiple or irregular	+	+
Ventral row stops short of anus by as much as four myomeres	+	+
Ventral row usually with fewer than 16 melanophores	+	+
Dorsal pigment row present	−	+
Dorsal row stops short of anus	−	+
Dorsal row multiple or irregular	−	+
Head or nape with at least some pigment	−	−
Head with two to five melanophores	−	−
Head with more than five melanophores	−	−
Lower jaw with some pigment	−	+
Hypural region with pigment spot(s)	−	+
Pectoral fins with some pigment	−	+

U.S. Bureau of Commercial Fisheries
Biological Laboratory, Seattle, Wash.

KENNETH D. WALDRON

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pp. 703–705

DAYTIME DISTRIBUTION OF *PONTOPOREIA AFFINIS* OFF BOTTOM IN LAKE MICHIGAN[1]

The vertical migration of the amphipod *Pontoporeia affinis* in Lake Michigan has been well documented by Wells (1960), Marzolf (1965), and McNaught and Hasler (1966). Wells and Marzolf observed *Pontoporeia* off bottom only at night. McNaught and Hasler, however, found *Pontoporeia* above the bottom shortly after noon in a 24-hr study on 12 June 1965, and some individuals were taken just below the thermocline in all daylight hours in a similar study on 19–20 August. This paper presents evidence that *Pontoporeia* regularly were present above bottom during the day from April–August 1964.

The data for this report were collected during a study of seasonal and depth distribution of larval bloaters (*Coregonus hoyi*) in Lake Michigan (Wells 1966). Sampling was conducted from the U.S. Bureau of Commercial Fisheries RV *Cisco* off Saugatuck, Michigan, at intervals of about 10 days from 9 April to 14 August 1964. A few samples were taken on 22 August and 15 October. Collections were made with a 1-m nylon plankton net (0.66-mm mesh) towed at 6.4 km/hr. Three days were usually required to complete a standard series of oblique tows at stations located at 5-fathom (9.1 m) intervals of bottom depth from 5 to 50 fathoms (9.1–91.5 m). The oblique tows at each station were made by 10-fathom (18.3 m) strata, except at depths not multiples of 10 fathoms, where the lowermost stratum was only 5 fathoms. The lower 1.5 m were not sampled in any stratum. For an "oblique tow," the net, as it was lowered, was towed 1 min at each of 11 equally spaced levels in the 10-fathom stratum being sampled, and then brought up at constant speed (combined boat and cable speed 6.8 km/hr). For 5-fathom strata the net was towed 1 min at each of six levels. No flowmeter was used, but clogging offered no problem; I assumed therefore that the volumes strained in different 5-fathom or 10-fathom strata did not vary significantly. Catches in the 5-fathom strata were adjusted to those of the 10-fathom strata in terms of organisms per 1,300 m^3 of water filtered (the approximate volume strained in an 18.3-m stratum, assuming perfect efficiency of the net).

All strata at a station were always sampled in full daylight of the same day. A bathythermograph cast was made at each station. Upon completion of a standard series, oblique tows usually were made in selected strata over bottom depths of 60 fathoms (109.7 m) and occasionally over bottom depths of 70 and 80 fathoms (128.0 and 146.3 m). For simplicity of presentation, further references to depth include only metric equivalents of measurements in fathoms recorded in the field. Complete details of the sampling procedures were described by Wells (1966).

The *Pontoporeia* in each tow were either counted or the number estimated. Collections during 9–12 April, 18–20 April, and 29 April–1 May were estimated in general terms of "few" or "many." Few indicated less than about 20, and many from about 20 to several hundred. Other estimates were usually made to the nearest hundred.

The plankton net lacked an opening-closing device; therefore, some *Pontoporeia* may have been captured as the net passed through strata above those being intentionally sampled. Contamination was considered insignificant, however, because *Pontoporeia* were far less abundant in the upper strata and because the net passed through upper levels rapidly in relation to its time in a sampled stratum below.

Pontoporeia were found above bottom over all depths of 36.5 m and greater (Table 1). None were off bottom over lesser depths, although they were abundant on the bottom to at least 18.3 m and a few were on the bottom at 5.5 m. *Pontoporeia* were off the bottom at all times of day, but these data are inadequate to

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[1] Contribution No. 378, Ann Arbor Biological Laboratory, U.S. Bureau of Commercial Fisheries.

TABLE 1. *Number of* Pontoporeia affinis *taken in oblique tows in different strata at various bottom depths and dates (1964). Catches in 9.1-m strata were adjusted to the 1,300* m^3 *of water filtered in the 18.3-m strata.*

[Estimates of numbers are indicated by F (few), M (many), and H (hundreds)]

Bottom depth (fathoms)	Bottom depth (m)	Stratum (m)	9–12 Apr	18–20 Apr	29 Apr–1 May	8–11 May	20–22 May	28–30 May	11–13 Jun	19–22 Jun	1–3 Jul	9–11 Jul	22–24 Jul	30 Jul–1 Aug	13–14 Aug	22 Aug	15 Oct
5	9.1	0–7.6	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–
10	18.3	0–16.8	–	0	0	0	0	0	0	0	0	0	0	0	0	–	–
15	27.4	0–16.8	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–
		18.3–25.9	0	0	0	0	0	0	0	0	0	0	0	0	0	–	–
20	36.6	0–16.8	F	F	F	3	6	0	0	0	0	0	0	0	0	–	–
		18.3–35.1	0	F	M	62	0	0	40	4	2	4	0	0	0	–	–
25	45.7	0–16.8	0	F	0	4	0	0	0	–	0	0	0	0	0	–	–
		18.3–35.1	0	F	F	18	2	1	3	–	0	0	0	0	0	–	–
		36.6–44.2	0	F	M	700	900	102	28	–	16	4	9	18	0	–	–
30	54.9	0–16.8	0	0	0	0	0	0	0	–	0	0	0	0	0	–	–
		18.3–35.1	0	0	0	26	0	2	1	–	0	0	0	0	0	–	–
		36.6–53.4	0	0	0	–	–	–	147	200	10	H	21	31	3	–	–
35	64.0	0–16.8	0	0	0	0	0	0	0	–	0	–	0	0	0	–	–
		18.3–35.1	F	0	F	6	0	0	0	–	0	–	0	2	0	–	–
		36.6–53.4	0	0	M	58	4	4	1	–	4	5	0	4	10	–	–
		54.9–62.5	0	0	M	262	29	98	98	–	54	16	33	33	91	–	–
40	73.2	0–16.8	0	0	0	0	0	0	0	–	0	–	0	0	0	–	–
		18.3–35.1	0	0	0	3	0	0	0	–	1	–	1	0	0	–	–
		36.6–53.4	0	F	F	26	6	0	0	5	2	4	0	0	1	–	–
		54.9–71.7	0	0	F	–	15	75	–	310	260	100	200	75	200	–	–
45	82.3	0–16.8	0	0	0	0	0	0	0	–	0	–	0	0	0	–	0
		18.3–35.1	0	0	0	0	0	0	0	–	1	–	0	0	0	–	0
		36.6–53.4	0	0	0	3	4	0	0	–	0	–	1	0	0	–	0
		54.9–71.7	0	0	0	20	10	4	13	–	0	18	18	18	8	22	0
		73.2–80.8	0	0	0	–	67	480	700	–	900	700	398	54	58	121	0
50	91.5	0–16.8	0	0	0	0	0	0	0	0	0	–	0	0	0	–	0
		18.3–35.1	0	0	0	0	0	0	0	0	0	–	0	0	0	–	0
		36.6–53.4	0	–	0	0	0	0	0	2	3	–	0	0	1	–	0
		54.9–71.7	0	–	0	0	3	0	2	11	100	17	9	0	5	13	0
		73.2–90.0	0	–	0	11	146	200	202	200	H	190	230	32	90	–	3
60	109.7	0–16.8	–	0	0	–	0	0	0	–	–	–	0	–	–	–	–
		18.3–35.1	–	0	0	–	–	–	–	–	–	–	0	–	–	–	–
		36.6–53.4	–	–	–	–	–	–	–	–	–	–	0	–	–	–	–
		54.9–71.7	–	–	–	–	–	–	–	–	–	–	4	–	0	–	–
		73.2–90.0	–	–	–	–	–	–	–	–	22	15	11	30	1	0	–
		91.5–108.2	–	–	–	–	300	–	H	–	300	H	H	H	50	500	–
70	128.0	0–16.8	–	–	0	–	0	0	0	–	–	–	–	–	–	–	–
		18.3–35.1	–	–	0	–	–	–	–	–	–	–	–	–	–	–	–
		73.2–90.0	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
		91.5–108.2	–	–	–	–	–	–	–	–	–	–	11	30	8	–	–
		109.7–126.5	–	–	–	–	15	H	H	–	–	H	H	300	H	–	–
80	146.3	0–16.8	–	–	0	–	0	–	0	–	–	–	–	–	–	–	–
		18.3–35.1	–	–	0	–	–	–	0	–	–	–	–	–	–	–	–
		128.0–144.8	–	–	–	–	–	–	H	–	–	–	–	–	–	–	–

show possible changes in depth distribution with time of day or light intensity.

Although the lack of counts in some catches prevents accurate comparisons of seasonal abundance, the records of Table 1 clearly show that the abundance of *Pontoporeia* off bottom generally increased from spring to summer and decreased in fall.

Pontoporeia in shallow areas reached highest abundance off bottom earlier in the season than did those in deeper areas. All catches through 29 April–1 May were at bottom depths of 73.2 m or shallower. Thereafter they were always caught at the deepest area sampled (down to 146.3 m). Numbers declined sharply at 45.7 m after 28–30 May, but large catches were made at 91.5 m until 22–24 July.

After 18–20 April, catches of *Pontoporeia* increased toward the bottom. The upper 18.3-m stratum produced only a few individuals (all over bottom depths of 36.6 and 45.7 m), and abundance was almost always highest in the sampling stratum nearest the bottom. Numbers in strata farther off bottom were usually largest over greater bottom depths. After mid-May, only a few individuals were taken in any stratum above the lowermost one at bottom depths of 73.2 m and shallower.

Data from several horizontal tows in mid-June (not tabulated here) provide information on the daytime distribution within the lowermost 18.3-m stratum above bottom at 73.2 m. Tows at 16.8, 12.2, 7.6, and 3.0 m above the bottom took 9, 76, 130, and 250 *Pontoporeia*, respectively (about 830 m^3 of water filtered per tow). Thousands of *Pontoporeia* usually were captured in tows of equal duration when the bottom of the net was towed (on runners) 0.3 m off the bottom.

The relationship between daytime vertical distribution of *Pontoporeia* and water temperature is difficult to assess because of the influence of light and the wide range of temperatures in the various strata, but a preference for cold water was obvious. Few individuals were taken from strata in which minimum temperatures exceeded 5C. The only *Pontoporeia* in any upper 18.3-m stratum were caught in the early spring when water temperatures were 4.7C or less. Several times in May, single individuals were caught in horizontal tows at the surface and at 1.5 m below the surface, in bright sunlight, where water temperatures were 3.4–3.9C. Horizontal tows at the surface in summer did not yield *Pontoporeia* in the daytime, but a few were caught at night at the surface in water as warm as 18.2C.

Pontoporeia above bottom in daytime, although occurring regularly, compose only a small fraction of the total population. Night tows usually yielded many times more individuals than tows at identical depths during the day. Horizontal tows with a 1-m net (830 m^3 of water filtered) in upper levels at night often caught several thousand *Pontoporeia.* Marzolf (1965) reported that the *Pontoporeia* migrating vertically at night represent only a small segment (never more than 7.4% in his study) of the total population.

LaRue Wells

Biological Laboratory,
Bureau of Commercial Fisheries,
Ann Arbor, Michigan 48107.

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Benthic Invertebrates of the New England Fishing Banks

by ROLAND WIGLEY

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Benthic Invertebrates of the New England Fishing Banks

by ROLAND WIGLEY

What does the sea bottom on the New England fishing banks look like? What kind of invertebrate animals dwell in these deep, cold waters?

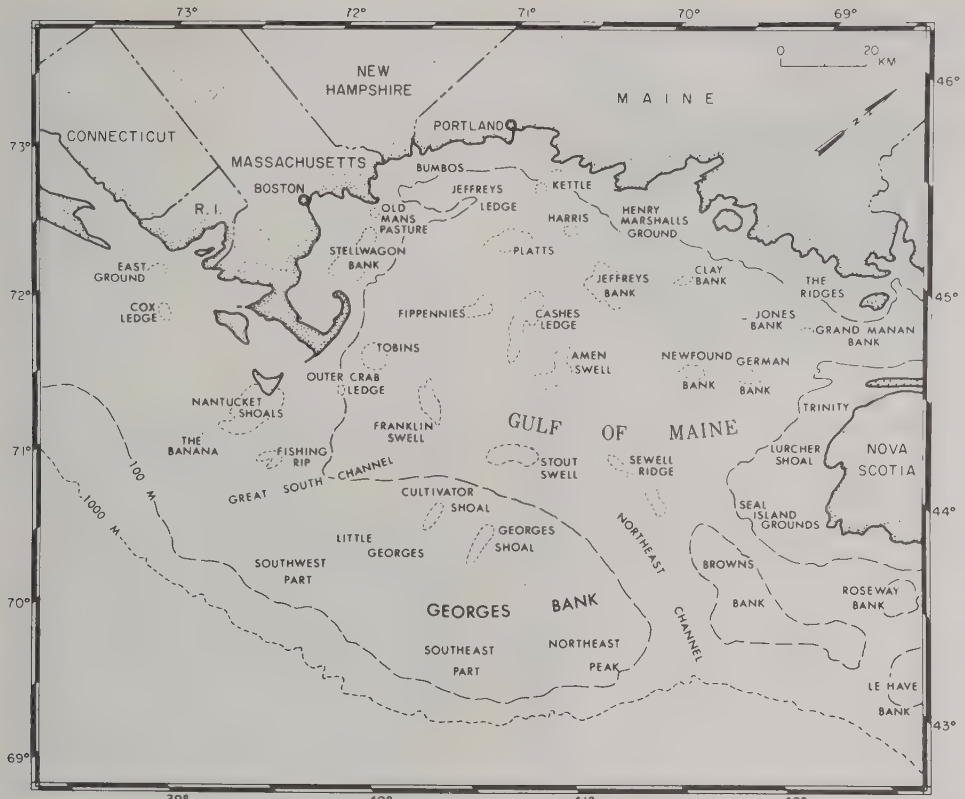
Curiosity about this fauna undoubtedly stems from many sources. One aspect of interest, and perhaps a source of wonder, is the enormous productivity of the New England fishing grounds — they rank among the richest fish producing areas in the world. Long before this country was settled, fishermen from Europe found the stocks of fish sufficiently plentiful to undertake a long and somewhat hazardous voyage across the Atlantic to harvest them. During Colonial times these populations of fish provided the basis for both domestic and foreign trade. Fishing, in fact, was one of the key industries that made possible the development of this country. Other industries such as shipbuilding, salt manufacturing, iron works, and lumbering, developed, in part, to provide the fishermen's needs.

Allied with the subject of productivity is the fact that most fishing in this region is for bottom-dwelling species —the so called groundfish or demersal fish. This is in contrast to the kind of fishing practised in many other parts of the world where pelagic species (tunas, anchovies, etc.) are the principal types that are sought. In New England, cod was the preferred species during the early period because of its good keeping qualities when salted and dried. Later on haddock, pollock, several species of hakes, and a number of different kinds of flounders made up the bulk of the commercial catch.

Each year about 1 million metric tons (2 billion pounds) of groundfish are harvested from the New England region. An adequate food supply for these fish is one of the vital necessities for their maintenance and growth. The food base for most of these groundfish is composed mainly of bottom-dwelling invertebrates, such as shrimps, crabs, worms, many kinds of mollusks, and echinoderms. Also, some of the less well-known invertebrate groups (brittlestars, holothurians, amphipods, mud shrimps) are important dietary items for certain species. Enormous quantities of these benthic organisms are necessary to support the large stocks of groundfish. The available food supplies are believed to affect some of the following: (a) observed differences in growth rate of fishes and their relative plumpness; (b) variations in the number of eggs produced and the survival of newly hatched young; (c) modifications in the normal migration routes and time of migration; (d) and, directly or indirectly, the survival of juvenile and adult stocks of fishes.

To provide information about the kinds and quantities of food organisms available to these vast stocks of groundfish, a study of the benthic invertebrate fauna was undertaken by the Bureau of Commercial Fisheries, with the close cooperation of the Woods Hole Oceanographic Institu-

Dr. Wigley is with the Biological Laboratories, Woods Hole, Mass. He is currently studying the productivity of marine fishes and their relationship to offshore benthic environments.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JONES BANK
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NEWFOUND BANK
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OUTER CRAB LEDGE
NANTUCKET SHOALS
TRINITY
FRANKLIN SWELL
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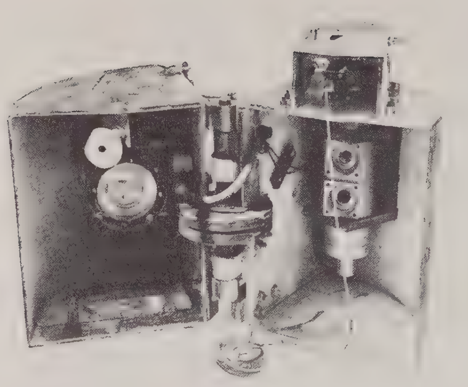
THE BANANA
FISHING RIP
LURCHER SHOAL
NOVA SCOTIA
GREAT SOUTH CHANNEL
STOUT SWELL
SEWELL RIDGE
100 M
CULTIVATOR SHOAL
1000 M
SEAL ISLAND GROUNDS
NORTHEAST CHANNEL
LITTLE GEORGES
GEORGES SHOAL
BROWNS BANK
SOUTHWEST PART
ROSEWAY BANK
GEORGES BANK
SOUTHEAST PART
NORTHEAST PEAK
LE HAVE BANK

Chart of the Gulf of Maine region off the northwestern coast of the United States showing a few of the many fishing banks and topographic features.

tion and the U. S. Geological Survey. The work of the latter two organizations in this study primarily concerns the broad geological aspects (see the article describing the Atlantic Shelf geology).

Several different kinds of instruments were used for sampling the benthic invertebrates because the size of these organisms ranges from large tree-like corals that may be 6 to 8 feet tall, down to small crustaceans and worms only 1/8 of an inch long or smaller. The small and medium-size organisms were collected with clamshell grab samplers (an example is the Campbell grab shown in the photograph). More than 1,000 samples, including sediment and the enclosed fauna, were collected with grab samplers from the area shown in the chart. The contents from the sampler were washed over a fine-mesh screen and all animals were picked out, classified, counted and weighed. Medium-size and large specimens were collected with Naturalist's dredges, scallop dredges, and large trawl nets (width of mouth opening 80 feet or more) of a type used by the trawler fleet. Several thousand dredge and trawl samples were collected from the area and handled in the same way that grab samples were processed. Information based on the samples has been supplemented by several thousand photographs of the sea bottom, and by visual inspection of the benthic environment from a research submarine. We thus have assembled sufficient information to give a general description of the varied and exceedingly fascinating animal life that



Bottom view of a Campbell grab sampler used for collecting quantitative samples of the benthic invertebrate fauna. Camera is installed in the righthand bucket, strobe light is in the lefthand bucket, and attached to the cord is a lead camera-tripping weight.

inhabits the banks and adjacent basins on the New England Continental Shelf.

The fishing banks off New England range in size from a few square miles, such as The Banana, Henry Marshalls Ground, Bumbos, and Old Man's Pasture, to such large plateau-like areas as Browns Bank and Georges Bank. Georges Bank is by far the largest fishing bank in this region. It is 150 miles long and 75 miles wide encompassing an area of roughly 10,000 square miles (more than the combined area of Massachusetts and Rhode Island). From one location to another within a fishing bank, or from one bank to another, there may be totally different types of bottom sediments, wide ranges in water depth, and different physical and chemical properties of the overlying water. The many diverse habitats resulting from these varied environmental characteristics have made it possible for an even wider variety of organisms to inhabit these areas. In spite of the risks of oversimplification, a general understanding of the banks fauna can be gained by considering a few of the more common and widespread faunal associations. It should be kept in mind, however, that overlap and intergradation of species is considerable between one faunal assemblage and another, and that exceptions occur to some of the broad statements concerning the geographic occurrence of particular faunas. Descriptions of the benthic invertebrate faunas that typically inhabit four common bottom types are given below in the following order: Sand Fauna, Silty Sand Fauna, Gravel Fauna, and Muddy Basin Fauna.

Sand Fauna

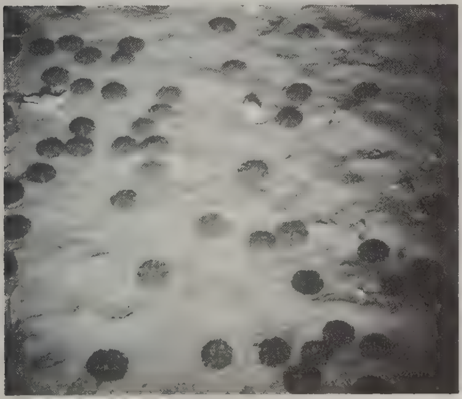
In large areas on the New England Banks the bottom is relatively free of silt and clay particles and is carpeted with sand. Water movements caused by wave action or by the strong tides typical of this region, and in some places by the nontidal water currents, have winnowed away the fine sediment particles leaving a rather "clean" sand. These areas are frequently in moderately shallow water atop the banks. In this type of habitat there live certain animals adapted to life in a loose and occasionally shifting sand substrate.

Some of the more common species in habitats of this type are: common sand-dollar, *Echinarachnius parma,* which is a thin, flat, circular echinoderm that rarely gets larger than 3 inches in diameter; sand shrimp, *Crangon septemspinosis,* a caridean decapod 2 to 3 inches long whose mottled coloration ranges from brown to nearly translucent white and blends in nicely with the sediment; two carnivorous gastropod mollusks — *Lunatia heros,* a large (2-1/2 inches) smooth-shelled species, and *Nassarius trivitattus,* a smaller (1 to 1-1/2 inches) rough-shelled form; surf clam, *Spisula solidissima,* a large (up to 7 inches) heavy-shelled bivalve mollusk that lives buried beneath the sediment surface; the chestnut astarte, *Astarte castanea;* small crustaceans such as *Leptocuma,* a cumacean, and *Chiridotea* an isopod; Acadian hermit crab, *Pagurus acadianus,* a relatively large species that utilizes gastropod shells for "houses"; various kinds of polychate worms *(Ophelia, Goniadella, Clymenella* and others); tunicates *Heterostigma* and *Molgula* that camouflage their nest with sand grains; and a variety of haustorid and phoxocephalid amphipods (beach fleas). Practically all of the above-named species are burrowing forms; some remain more or less permanently beneath the sediment surface and others burrow only occasionally as conditions demand. Also, a large proportion of these animals are translucent or light in color; often whitish.

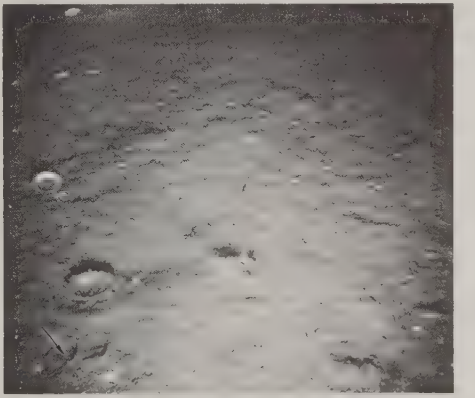
Typical localities where this type of fauna occurs are as follows: Nantucket Shoals region, central part of Georges Bank, central and eastern parts of Browns Bank, Stellwagen Bank, parts of Lurcher Shoal, and other similar places.

Silty Sand Fauna

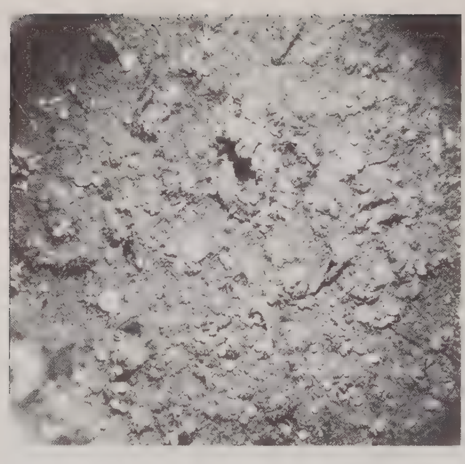
Bottom deposits at moderately shallow depths around the periphery of some fishing banks are frequently composed of mixtures of sand, silt, and clay. This type of bottom, referred to as silty sand, has a loose, pliable surface. Weak to moderate water currents that flow over these deposits are rich in plankton and deritus. Substantial portions of this suspended matter settle out and serve as food for the deposit-feeding invertebrates. Other suspended components are removed directly from the water by filter-feeding species. The fauna inhabiting silty sand sediments is composed of a group of animals intermediate in form, structure, and habits between those living in silt-free sand and those from the muddy basins (see below), and some of the species from these other sediment types commonly occur in silty sand. Although the species composition of this fauna is not nearly as varied as that of the gravel fauna (see below) it is moderately rich in species and frequently contains



An oblique view of the sea bottom near the central part of Georges Bank shows sand ripples and some common invertebrate animals that inhabit sand sediments. The dark disk-shaped objects are sand-dollars; the light-colored rounded mollusks are moon shells; the small white elongate snail (near lower right) is a dog whelk; the starfish is a medium-size specimen of northern starfish; and on the righthand side of the picture just below the middle are several small specimens of Acadian hermit crabs.



An oblique view of the sea bottom on the southern side of Georges Bank showing a silty sand habitat and some of the animals that live there. The bivalve shells are from dead specimens of ocean quahogs; in the lower center is a shell from a long-dead ten-ridged neptune (snail); along lefthand side are four northern starfishes; and tubes of amphipods and polychaete worms are numerous. Also, at least a dozen pandalid shrimp are in this picture (see arrow); how many can you find?



A dense assemblage of animals on a gravel substrate is shown in this close-up vertical view of the sea bottom near Grand Manan Bank (northern Gulf of Maine). The numerous small white objects are brachiopods (lamp shells), the larger light-colored animals are sponges and an Iceland scallop, and the other common forms are bryozoans and polychaete worms.

No animals are visible in this close-up view of a mud-bottom area in the Gulf of Maine, but evidence of animal life is revealed by the tubes of amphipods (beach fleas) and polychaete worms, and by the tracks and burrows in the sediment. The object in the lower lefthand corner is the camera-tripping weight.

a large number of individuals of a few kinds — burrowing forms and tube-dwelling species are particularly abundant.

Some of the common inhabitants of the silty sand sediments are: ocean quahog, *Arctica islandica,* a rather heavy-shelled bivalve mollusk that is similar in size and habits to the shallow-water quahog or hard-shell clam from which it differs by having a thick, dark periostracum; rough-skinned thyone, *Thyone scabra,* a spindle-shaped burrowing sea cucumber 2 to 3 inches long with the body surface covered with short papillae; *Ampelisca vadorum* and *A. compressa,* small (1/4 to 1/2 inch) tube-dwelling amphipod crustaceans that are exceedingly numerous and an especially important food for groundfish; other common crustaceans — the decapod shrimp *Dichelopandalus,* the cumacean *Diastylis,* the isopod *Edotea;* polychaete worms such as *Scalibregma, Nepthys, Harmothoe,* and many others; a burrowing sea anenome *Cerianthus* that has long slender tentacles gracefully arched toward the water current; brittlestars *Amphioplus* and *Amphilimna* that crawl on and through the sediments; pygmy distaff shell *Colus pygmaeus,* a small (1 inch) carnivorous gastropod; and many small to moderately small bivalve mollusks such as *Venericardia, Nucula,* and *Crenella.*

Localities where this fauna occurs are the deeper areas around Nantucket Shoals, the shelf area off southern New England, and along the southern side of Georges Bank. Somewhat similar faunas inhabit silty-sand sediments in the vicinity of many banks in the Gulf of Maine.

Gravel Fauna

A large number of banks in the Gulf of Maine region are floored with gravels that range in size from pebbles to boulders. Also, in a few areas, ledges of bedrock outcrop on the ocean bottom. The velocity of the waters flowing over these rocky areas is usually moderate to strong. With few exceptions, this combination of physical features forms suitable habitats for colonization by sessile organisms that require a firm substrate for attachment and a food supply brought to them by the passing currents. This assemblage not infrequently develops into densely clustered masses of animals, including many colonial forms, that represent a wide diversity of taxonomic groups.

Some of the common components of the gravel fauna are: sponges, such as *Polymastia, Clionia,* and *Myxilla;* barnacles, *Balanus crenatus* and *B. hameri;* a great variety of beautifully shaped and delicately colored hydroids —*Tubularia, Eudendrium, Sertularia,* and *Bouganvillia,* to name a few; the lampshells *(Brachiopoda)* represented mainly by *Terebratulina;* soft corals only a few inches high *(Gersemia)* as well as others which attain a size comparable with that of small trees *(Paragorgia);* tunicates, represented by the solitary forms *Boltenia* and *Ascidia,* and colonial types like *Amaroucium;* filter-feeding bivalve mollusks, *Modiolus, Placopecten, Anomia and Musculus;* polychaete worms, *Serpula, Chone, Spiorbis,* and related kinds characterized by beautiful branchial plumes, plus numerous errant forms; rather large carnivorous motile forms such as the starfishes *Solaster* and *Crossaster,* the gastropod *Neptunea,* and the toad crab, *Hyas;* various kinds of nudibranchs *(Doris, Dendronotus,)* and brittlestars *(Ophiopholis, Ophiacantha).* This abundant and varied assemblage of benthic invertebrates form one of the richest and most complex — and highly interesting — faunal groups to be found on the New England banks.

Gravel faunas are abundantly represented on Cashes Ledge, parts of Great South Channel, the northeastern part of Georges Bank, western Browns Bank, Jefferys Ledge, and numerous other smaller banks in the Gulf of Maine region.

Muddy Basin Fauna

In the deepwater basins between the fishing banks the sea bottom is blanketed with fine-grained sediments commonly referred to as mud. The major constituents of the mud are silts and clays, plus a smaller amount of fine sands. Water currents in these mud-bottomed basins are weak and the sediment surface is generally level and smooth. Some of the animals, especially crustaceans and polychaete worms, have long delicate legs, tentacles, or other appendages suitable for moving about or feeding in this soft-bottom environment. The number of different kinds of animals as well as the density or abundance of all species combined is low in comparison with that on the fishing banks.

Species of benthic invertebrates that are common inhabitants of the muddy basin areas are: *Briaster fragilis,* a heart urchin of moderate size (up to 3 or 4 inches) that burrows into the sediment and remains below the sediment surface; *Ophiura sarsi, O. robusta,* and *Amphiura otteri,* brittlestars that as adults range in diameter from about 3 to 12 inches; *Ctenodiscus crispatus,* mud star, a pentagonal-shaped starfish that derives its nourishment by engulfing the muddy sediment; *Modiolaria discors,* a small (1/2 inch) bivalve mollusk; *Scaphander,* a gastropod mollusk; *Cadulus* and *Dentalium,* scaphopod mollusks that are sometimes termed tusk shells; *Haploops tubicola,* a small (1/4 inch) tube-dwelling amphipod; *Munnopsis typica,* a delicate limbed isopod crustacean; decapod crustaceans—*Calocaris, Geryon,* and *Pandalus;* the solitary ascidian *Polycarpa fibrosa;* and a number of different kinds of polychaete worms, such as *Sternaspis, Amphitrite, Onuphis, Leanira,* and others. A rather large proportion of the animals mentioned above are deposit feeders; some feed indiscriminately on the sediments and others select particular portions of the sediment. Carnivores constitute the other main group of animals.

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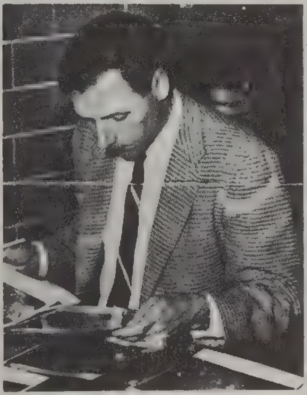
Can submersible vehicles be used effectively in studies of cold water shelf fisheries?

By ROLAND L. WIGLEY



The writer of this article is Chief of the Benthic Invertebrates Project at the US Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts. Dr. Wigley studied at Cornell University where he obtained a Ph.D. (icthyology). He joined the US Fish & Wildlife Service as a fishery research biologist in 1953.

The main project currently in progress under his direction is a quantitative study of macrobenthic organisms inhabiting the continental shelf and slope off the east coast of the United States, from Canada to Key West, Florida.

This is being done in co-operation with the US Geological Survey and the Woods Hole Oceanographic Institution. A total of 2,000 quantitative samples has been collected by five research ships on 22 cruises.

In addition to an inventory of food resources available for fish, the study is providing: (1) information on un-utilized invertebrate stocks; (2) a basis for delineating faunal provinces; (3) information for evaluating the effects of environmental characteristics on species and higher taxa of benthic animals; (4) specimens for detailed biological studies of individual species. Forty-five zoologists at museums, universities and research institutions in the United States and other countries are co-operating in this study.

A RECENT dive in the research submarine *Alvin*, (Woods Hole Oceanographic Institution's deep submergence vehicle) contributed to a new insight into the possible uses of underwater vehicles in fishery research

It has been repeatedly shown in recent years that manned underwater vehicles can operate effectively in the clear waters of the tropics and great ocean depths, and that direct observations made from these vehicles can be extremely valuable. Some of the questions or problems that ordinarily necessitate repetitious, time-consuming sampling from conventional surface vessels can be quickly and authoritatively answered by a simple, direct observation. Can these same direct techniques be applied to fishery investigations under less favourable conditions?

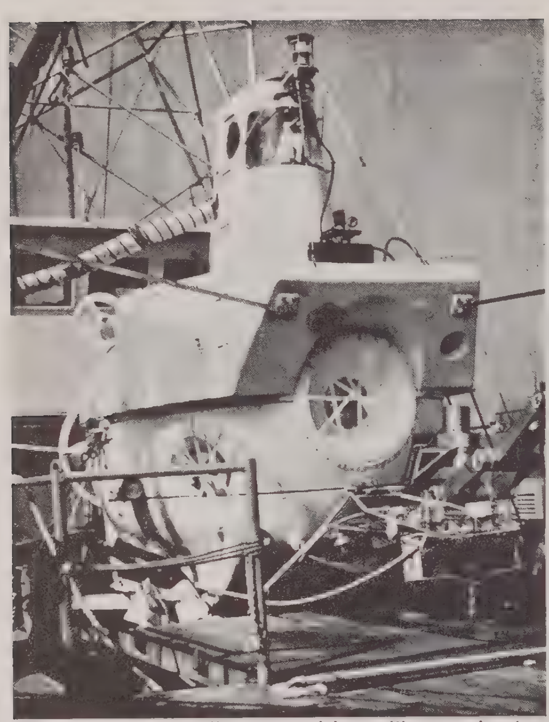
Many of the great fisheries of the world concentrate their efforts in particular portions of the plankton-rich continental shelf waters of the temperate and sub-polar regions. Underwater visibility is notoriously poorer in such areas than in oceanic waters that are far removed from sediment-laden runoff from land.

Visibility

Plankton and organic detritus — which are closely associated with fish production — and suspended sediment are the very components that contribute heavily to restricting underwater visibility. Consequently, there has been much speculation concerning the utility of submersible vehicles in fishery research in areas where these restricting conditions prevail. Other physical aspects that frequently hamper fishery studies in continental shelf areas are rough, irregular topography of the sea bottom and strong water currents.

A dive in the *Alvin* on Georges Bank clearly demonstrated that underwater vehicles of this type can be used effectively under rather severe operating conditions. Georges Bank is an exceptionally productive fishing ground on the New England continental shelf east of Massachusetts. Cod, haddock, herring, and various species of hakes and flatfishes are abundant there, and the waters are rich in plankton.

On August 30, 1967, I participated in a five-hour dive on the western side of Georges Bank. The dive was made in collaboration with Dr. K. O. Emery and Mr. James V. A. Trumbull, scientists at the Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.



The "Alvin" before dive, secured in position on elevator aboard the mothership "Lulu". Tape temporarily criss-crosses viewing ports to protect against accidental scratches on window surfaces.

Launched

Weather conditions were excellent; it was sunny and clear and the sea was nearly calm. The R/V *Lulu*, a 96-ft. catarmaran that admirably serves as the *Alvin's* mother-ship, rocked slowly and gently in the vicinity of the dive site. A superb crew (of Palomares H-bomb fame) made numerous pre-dive checks — operations reminiscent of flight preparations for military aircraft. Following the check-out, the *Alvin* was launched and descended slowly to sea bottom, a depth of only 60 metres — which is very shallow compared with most of her dives.

Subsurface cruising conditions were much less favourable than they were at the surface: (1) Visibility was limited (chiefly by plankton) to a distance of about seven metres; (2) on reaching bottom we immediately encountered rather strong water currents (up to 1½ knots); and (3) the presence of large boulders — dropped thousands of years ago by retreating glaciers — every hundred metres or so made a very slow cruising speed along the sea bottom mandatory. (Except for the boulders, the bottom was flat and carpeted with clean pebbles two to five centimetres in diameter).

Plankton was present from surface to bottom without evident discontinuity. This widely distributed mass of microscopic and macroscopic life produced a "haze" or interference to underwater viewing. This interference became extraordinarily accentuated when the lights just outside the viewing ports were on and the vehicles was moving directly into the current. The bright light, however, provided a good opportunity to ascertain the general composition of the macroplankton. Copepods and chaetognaths (arrow worms) were the dominant components. Some of the less common animals were jelly-fishes, crab larvae, larval fish, and juvenile stages of euphausiids or mysids.

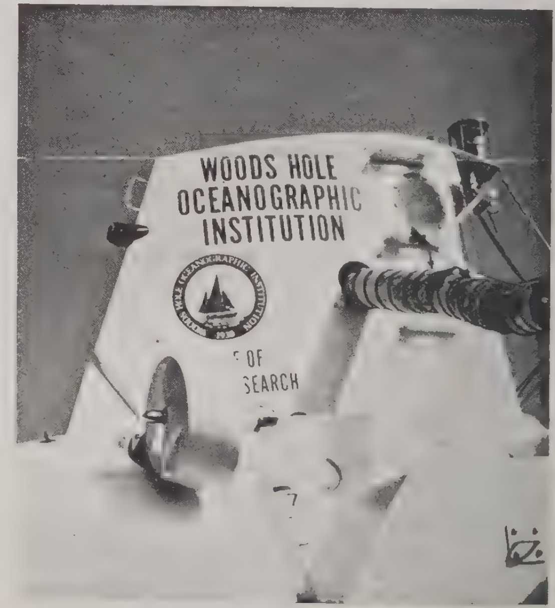
Benthic invertebrates

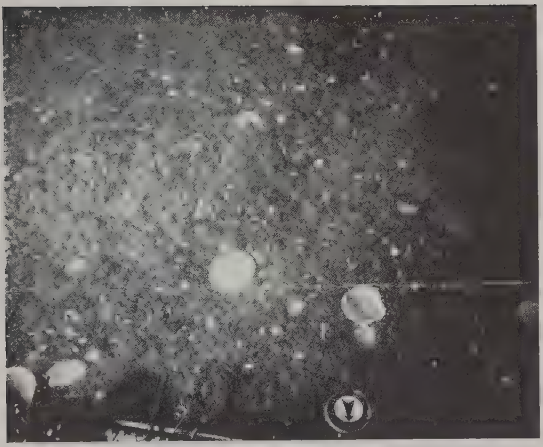
One community of benthic invertebrates was distributed throughout the entire area traversed during the dive. Species characteristic of this community were: sea scallop (*Placopecten*), waved whelk (*Buccinum*), northern heart shell (*Venericardia*), slender-armed sea star (*Leptasterias*), green sea urchin (*Strongylocentrotus*), Acadian hermit crab (*Pagurus*), and encrusting bryozoans (*Ectoprocta*).

Sea scallops are known to occur in commercial quantities over large areas of Georges Bank. Making use of this valuable resource is a fleet of scallopers from the United States and Canada. Both countries are engaged in research on the biology and population trends of this species. Since market-sized specimens can be readily spotted from the submarine, it may be possible to obtain the necessary information on changes in abundance, predators, new beds, and related aspects, much more quickly from a submersible than by conventional methods.

Many fish could be seen and most could be readily identified in spite of the unfavourable conditions for operating

The "Alvin's" sail section with air conditioning duct leading through port to the operators' compartment below. Constant precautions are necessary to control humidity, because of the sensitive electronic gear.





Sea bottom at a depth of 60 metres on the western side of Georges Bank. Photograph taken from the "Alvin" shows living sea scallops and shells of dead specimens. Living specimen in centre is approximately 15 centimetres in diameter. Compass and sampling apparatus at bottom of picture are attached to the "Alvin's" equipment rack.

a small submarine and the limited visibility. Roughly 150 fish were sighted, including both pelagic and demersal species. Most were between 30 and 50 centimetres long; the largest were about 70 centimetres.

The pelagic types consisted of two schools — one of herring (*Culpea*) and the other of mackerel (*Scomber*). Because of the rapidity with which these groups passed over the submarine, the accuracy of the identifications is open to question.

Demersal fish, which accounted for the bulk of all fish in the area surveyed, were more easily and reliably identified. They typically either remained stationary or swam slowly enough to permit the observer to have a careful look; over 95 per cent were identified to genus and over 85 per cent to species. A total of 14 species, representing 10 different genera, of bottom-dwelling fishes were recognized.

All of the large, commercially important, species (haddock, silver hake, winter flounder, eelpout) were easily identified. Generally it was the smaller specimens (*sculpins*) or the groups that consist of several closely similar species (*skates*) that were most difficult to determine to species. Special training and additional experience would, of course, increase efficiency in recognizing these more difficult groups.

As a result of this experience, it appears highly feasible to use submersible vehicles to census demersal fish and the large benthic invertebrates (sea scallop, starfish, etc.) in the Georges Bank area, or other similar continental shelf regions.

A submersible vehicle obviously could not be expected to be used in all aspects of offshore fishery research. It is an additional tool — a modern, exceedingly useful tool — that will help fishery scientists answer the innumerable questions about the lives of fishes and their response to the environment.

The use of a submersible such as the *Alvin* would speed the gathering of basic information. The fishermen and the industry as a whole would be provided with facts before or during the occurrence of significant biological phenomena, so that measures could be instituted immediately, if necessary (or as soon thereafter as required), to take advantage of the observed changes.

(63)

Compartmental Analysis of Production and Decay of *Juncus roemerianus*

RICHARD B. WILLIAMS, *Oak Ridge National Laboratory,*
and MARIANNE B. MURDOCH,
U. S. Bur. Commercial Fisheries

The rates of annual net production and decay of *Juncus* (needle rush) in a salt marsh near Beaufort, N. C. were determined by fitting field data into a compartmental model in which individual culms moved through three successive compartments: live, dying and dead. Average standing crops (dry wgt./m^2) for the compartments were respectively, 340 g, 500 g, and 1600 g; the number of turnovers per year were respectively, 2.5, 1.7 and 0.53. Annual production was 850 g (dry wgt.)/m^2. The rate of production was greatest in summer and least in midwinter.

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Standing Crop and Importance of Zooplankton in a System of Shallow Estuaries[1]

Richard B. Williams
Marianne B. Murdoch
Leon K. Thomas[2]

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Standing Crop and Importance of Zooplankton in a System of Shallow Estuaries[1]

Richard B. Williams
Marianne B. Murdoch
Leon K. Thomas[2]
Bureau of Commercial Fisheries
Radiobiological Laboratory
Beaufort, North Carolina 28516

ABSTRACT: A yearlong study of the general taxonomic composition and standing crop of zooplankton was made in a system of shallow estuaries near Beaufort, N. C. Ten stations were sampled with a No. 10 net at 5-week intervals. Copepods predominated; meroplanktonic larvae were second in importance. Standing crop ranged from 0.002 to 0.46 ml/m^3 (displacement volume). Averages for the stations ranged from 0.089 to 0.149 ml/m^3 and were not significantly different from one another. Averages for the surveys ranged from 0.033 ml/m^3 in July–August to 0.285 in January. The standing crop was significantly greater in the winter than in the late summer. The annual average, 0.114 ml/m^3, multiplied by the average depth of the estuaries, 1.18 m, yielded a standing crop of 0.13 ml/m^2.

Comparison of our data with other studies suggested that a small standing crop of zooplankton was typical of shallow embayments. For areas other than the open sea, standing crop was approximated by the equation:

$$\text{Zooplankton vol. (ml/m}^2) = 0.259 \times \text{avg length water column (m)}^{1.145}$$

Factors responsible for the scarcity of zooplankton in the Beaufort area were not identified, but temperature, food supply, and tidal flushing were eliminated as potential factors. Daily food consumption by zooplankton was estimated to be only 2 to 9% of the phytoplankton net photosynthesis. In shallow areas the importance of zooplankton as a part of the herbivore link in the food chain appeared inversely related to the average length of the water column.

Introduction

The sequence, phytoplankton—zooplankton—carnivores, forms the classical food chain for the aquatic environment. Although the validity of this sequence for the open sea is unquestioned, studies on Long Island Sound (Riley, 1956) and the English Channel (Harvey, 1950) indicated that even in these areas, 20 and 70 m deep respectively, benthic animals are important consumers of phytoplankton. The significance of zooplankton as an intermediate step between phytoplankton production and carnivore production in shallower marine areas has not been examined previously. A yearlong study of plankton in a system of shallow estuaries near Beaufort, N. C. (Williams, 1966) provided an opportunity to make simultaneous observations of phytoplankton production and the standing crop and taxonomic composition of zooplankton. These observations permitted us to deduce the probable importance of zooplankton in the total energy flow of the area studied.

Previous work on the standing crop and taxonomic composition in estuarine zooplankton in the Beaufort area consisted of detailed observations at a single location on the species present and their abundance in terms of organisms per cubic meter of water (Sutcliffe, 1948, 1950). Studies on other inshore areas along the eastern sea-

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[1] This research was supported through a cooperative agreement between the U. S. Fish and Wildlife Service and the U. S. Atomic Energy Commission.

[2] Present adress: Coast Guard Division 13, APO San Francisco, California 96291.

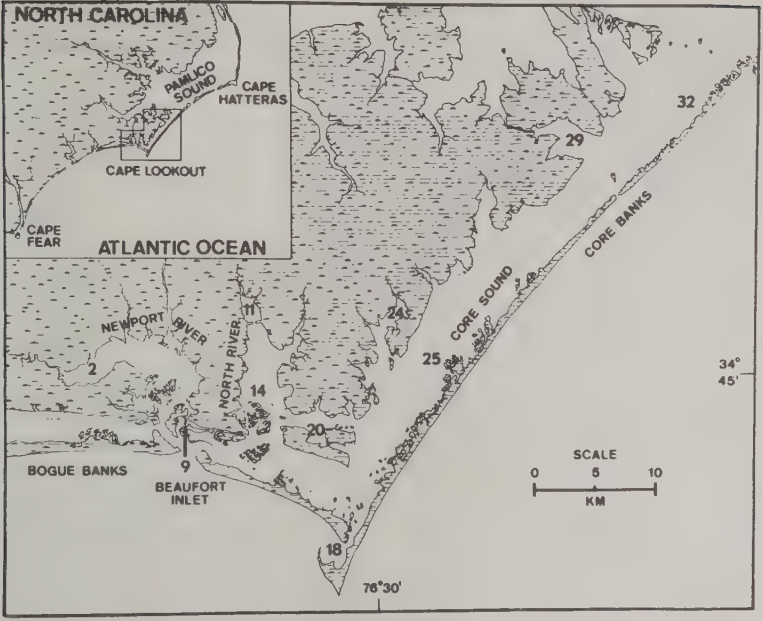
NORTH CAROLINA
PAMLICO SOUND
CAPE HATTERAS
CAPE LOOKOUT
CAPE FEAR
ATLANTIC OCEAN
32
29
CORE BANKS
CORE SOUND
24
25
11
NEWPORT RIVER
NORTH RIVER
2
14
20
9
BOGUE BANKS
BEAUFORT INLET
18
34° 45'
76°30'
SCALE
0 5 10
KM

Fig. 1. Map of the area studied. Locations of zooplankton sampling stations are indicated by the positions of the station numbers.

board of the United States have yielded very diverse estimates of zooplankton biomass. The range was from approximately 0.14 ml/m^3 in a 1-m-deep Cape Cod salt pond (Barlow, 1955) to 0.95 ml/m^3 and 19 ml/m^2 in Long Island Sound (Deevey, 1956).

We thank the many individuals who aided in the completion of this study. W. D. C. Smith, T. G. Roberts, and others at the Radiobiological Laboratory assisted with the field work; K. J. Fischler provided advice on statistical methods. Dr. R. J. Conover (Bedford Institute of Oceanography, Dartmouth, Nova Scotia) and Dr. H. P. Jeffries (University of Rhode Island) read preliminary drafts of the paper and suggested many improvements.

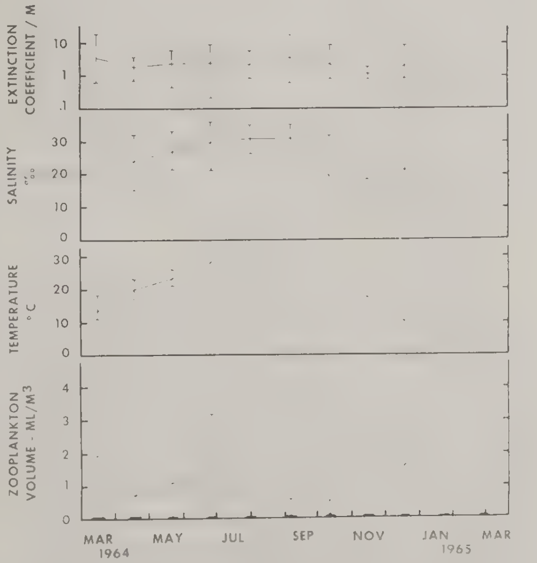

Fig. 2. Average values for each survey for extinction coefficient, salinity, temperature, and standing crop of zooplankton. Vertical bars indicate the range of values; thickened segments of the abscissa indicate the duration of the surveys.

The Area Studied

The area is a portion of the series of embayments extending southwest from Pamlico Sound behind a chain of barrier islands (Fig. 1). The hydrography of the area, which was described by Williams (1966), is summarized below and in Fig. 2. The values in this paper differ slightly from those in Williams (1966) because of the omission of observations from stations where zooplankton was not sampled. One of the channels connecting the estuaries with the ocean reaches a depth of 13 m, but most of this 400 km^2 area does not exceed 2 m in depth. The average depth at half tide is 1.18 m and the tidal range is around 0.8 m. Wind action and tidal currents tend to prevent vertical stratification of the water. Average temperature followed a normal seasonal cycle, ranging from 28 C in June to 8 C in January. The shallowness of the water, however, permitted temperature differences as great as 8 C between different parts of the area visited a few days apart. Close to the ocean, salinity remained in general at least 30‰; but at the heads of the estuaries, salinity fluctuated widely in response to variations in freshwater inflow. Light penetration, like temperature and salinity, was widely variable. Extinction coefficients were lowest near the ocean, and increased toward the heads of the estuaries. This increase was due to the brown stain of the freshwater influx, and the change in the character of the bottom sediments from sand and shell near the ocean to increasingly muddy material toward freshwater. The softer sediments were easily suspended by waves and currents. Extinction coefficients per meter ranged from 0.2 to 17; average extinction coefficients ranged from 1.1 to 3.6 and had no obvious seasonal cycle.

Methods

Zooplankton was collected quantitatively with a Clarke-Bumpus sampler previously calibrated by towing it without a net over a course of known length (Clarke and Bumpus, 1950). Samples were taken with a No. 10 net at about 5-week intervals from March 1964 to March 1965 at each of 10 stations (Fig. 1 and 2). Tows long enough to filter about 5 m^3 (range 3.25 to 6.00 m^3) were made at mid-depth at each station. Plankton was preserved immediately with formalin. At the laboratory, samples were examined with a dissecting microscope, the more abundant taxa noted, and an estimate made of the relative volumes of zooplankton, phytoplankton, detritus, and sand. Fish beyond the larval stage and large medusae were picked from the samples before the total displacement volume of the remaining material was measured by the method of Yentsch and Hebard (1957).

Seven of the 110 samples could not be used for measurements of plankton abundance either because of mechanical difficulties with the sampler or because the sample contained an abundance of the large ctenophore, *Mnemiopsis*. These organisms disintegrated in formalin, converting a sample into a syrupy mass not filterable through the fritted glass bottom of the original measuring chamber. Midway through the study, however, we found that replacement of the fritted glass with No. 10 netting permitted withdrawal of the ctenophore-thickened liquid, and measurement of zooplankton volume despite the presence of ctenophores.

Measurements of zooplankton displacement volume were converted to estimates of weight by the relationship: 1 ml is equivalent to 85 mg dry weight (95% confidence limits, 58 and 113 mg). This relationship, similar to those obtained previously by Deevey (1952) and by Menzel and Ryther (1961), was determined by measuring the volume of four samples containing no appreciable quantity of material other than zooplankton, rinsing the zooplankton free of sea water, and drying it at 100 C.

TABLE 1. Percentage of samples having various percentage volumes of zooplankton.

Percentage of volume of sample contributed by zooplankton	Percentage of samples
100	4
90–99	25
70–89	27
50–69	15
0.5–49	29

Results and Discussion

COMPOSITION AND STANDING CROP OF THE ZOOPLANKTON

Zooplankton other than large medusae and ctenophores constituted the bulk of the material retained by the No. 10 net in 71% of the samples (Table 1). In 16%

TABLE 2. Volume of zooplankton (ml/m³) and taxa forming at least half the volume. Legend: Taxon not indicated = copepods; C = holoplanktonic crustaceans; L = meroplanktonic larva of benthic animals; F = fish eggs and larva; A = caprellid amphipods; S = *Sagitta*. Asterisk indicates that zooplankton formed less than half the volume of the material retained by the net. Line indicates that plankton volume was not measured.

Station No.	Mar.	Apr.	May	June	July–Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
2	0.04*	0.06	0.002* C	0.32	0.01 L	— C	—	0.12	0.22	0.44	0.13
9	.06*	.04	.10	.11 C	—	.04 C	.10	.02* C	.06 C	.46	.32*
11	.13	.06	.16	.02* C	.04	.03*	.08*	.12	.07*	.29*	.10
14	.17	.12	.20	.10* F	.02	.09	.09	.09	.04*	.40	.10*
18	.09*	.05	.12	.28 C	.07 C	.06* A	.04	.05 C	.01 S	.10	.11
20	.19	.10	.11	.05 L	.07 L	.002*	.02	.12	.13	.08*	.21
24	.03*	.08	.03 C	.06	.05*	.09* C	.11*	.10	.22	.11*	.29
25	.03* C	.05	.26*	.08 L	.02	.01	.01	.11	.24	.32	.15
29	— L	—*	.04*	.04	.01	.05	.01	.17	.33	.43*	.08*
32	— L	—*	.08	.10	.01 C	.13	.01* L	.16	.26	.22*	.27
Mean	0.092	0.070	0.110	0.116	0.033	0.056	0.052	0.106	0.158	0.285	0.176

of the samples, large medusae and ctenophores composed the bulk of the catch; in 7%, detritus; and in the remaining 6%, mixtures of phytoplankton, sand, jellyfish, and detritus.

Copepods dominated the zooplankton community. They formed at least half the measured volume in 87 of the 110 samples, in the majority of samples at every station, and at the majority of stations in every survey except June (Table 2). Mixtures of crustaceans—ostracods, cladocerans, and substantial numbers of copepods—formed the bulk of the volume in 13 samples. Meroplanktonic larvae of barnacles, decapods, molluscs, and annelids were dominant in 7 samples, and caprellid amphipods, a chaetognath (*Sagitta*), and fish eggs and larvae were dominant in 1 each. The amphipods, which normally cling to plants, apparently were swept into the open water of Lookout Bight (Station 18) by a strong tidal current. The tunicate *Oikopleura* was common in many samples, but never dominant.

In every survey the abundance of zooplankton varied widely among the stations, and without apparent pattern (Table 2). Averages for the entire study, however, ranged only from 0.089 ml/m³ at Station 18 to 0.149 ml/m³ at Station 2. An analysis of variance done by transforming values given in Table 2 to logarithms and calculating approximations for the seven missing observations by the method of Yates (see Goulden, 1952: 320) indicated no significant differences among the station averages. Therefore, the station averages were pooled, and a grand average of 0.114 ml/m³ was obtained. This value times the average depth of the area studied, 1.18 m, yielded a standing crop of 0.13 ml/m².

Averages fluctuated seasonally around the general average of 0.114 ml/m³ (Fig. 2). Volumes were generally greatest in the winter (December–February) and least in late summer and early fall (July–October). The existence of smaller irregularities in the seasonal trends, however, such as the secondary peak in May and June, was unproven. Each of the survey means (Table 2) except the largest and smallest, January and July–August respectively, was not significantly different from the means for six to eight other surveys (as determined by the multiple range test as modified by Kramer, 1956). There is no reason to believe that the seasonal fluctuation observed in our study must invariably be repeated as an annual cycle. Sutcliffe (1950) reported zooplankton most numerous in the Beaufort Channel (Station 9) during the summer.

ACCURACY IN ESTIMATING STANDING CROP

The data obtained in our survey (Table 2) formed a coherent picture. The range in standing crop was 0.002 to 0.47 ml/m^3. About half the observations lay within ±50% of their respective survey means, and within ±50% of the arithmetic annual mean, 0.114 ml/m^3. Most of the observations greater than 0.17 ml/m^3 (0.114 + 50%) were made during the three surveys with the highest means, December through February, and most of the observations below 0.06 ml/m^3 (0.114 − 50%) were made during the three surveys with lowest means, July–August through October. Our results were thus sufficiently consistent that it seems unlikely that increasing the number of observations by adding more stations or more surveys would have yielded markedly different results.

The Clarke-Bumpus sampler used in this study, despite its small diameter, appears to capture most of the zooplankton (Barnes and Tranter, 1965). Even slight clogging of a No. 10 net may not greatly reduce the sampler's capacity to capture estuarine forms; Heinle (1966) found no significant difference in the catch of adult *Acartia* between samplers equipped with No. 10 and No. 20 nets. Our calibration of the Clarke-Bumpus sampler was slightly in error since, even without a net, the sampler does not accept all the water in its path. This error, however, should not exceed 7% (Yentsch and Duxbury, 1956).

It is unlikely that visual estimation of the portion of total displacement volume represented by zooplankton introduced important errors. Presumably the smaller the proportion of extraneous material, the greater the accuracy in determining zooplankton volume. If only the 73 samples that consisted of at least 50% zooplankton were used, the annual average would be 0.131 ml/m^3; if only the 44 samples that consisted of at least 80% zooplankton were used, the annual average would be 0.135 ml/m^3. These figures are little different from the 0.114 ml/m^3 obtained by using all the samples.

COMPARISON WITH OTHER STUDIES

The major characteristics of this zooplankton population—a general dominance by copepods, the occasional abundance of other taxa, and much variation in total volume—agree with Sutcliffe's (1950) earlier study of the Beaufort area and appear normal for inshore areas in general. The results of a number of zooplankton investigations conducted mostly on the Atlantic and Gulf coasts of the United States are summarized in Table 3. Irregular variations in total plankton volume characterized all these studies. Copepods dominated the zooplankton in 9 of the 10 studies cited in Table 3 that contained taxonomic information, and in studies of a Massachusetts salt pond (Deevey, 1948), an arm of Chesapeake Bay (Heinle, 1966), Biscayne Bay, Florida (Reeve, 1964), and the Mississippi River Delta (Cuzon du Rest, 1963). Other forms such as chaetognaths, ctenophores, medusae, tunicates, amphipods, mysids, and meroplanktonic larvae were occasionally very abundant.

Although the taxonomic composition of our samples was in no way unusual, the standing crop of zooplankton was uncommonly small. Both our average standing crop, 0.114 ml/m^3, and our maximum standing crop, 0.46 ml/m^3, are smaller than those obtained in the 12 other inshore studies (Table 3). The average standing crops in the 12 studies range from 20 to 800% greater, and averaged 400% greater. Only oligotrophic mid-ocean areas, the Sargasso Sea and the tropical eastern Pacific, have values for zooplankton standing crops per cubic meter lower than ours. Thus, when length of the water column is taken into consideration and volume of zooplankton computed per square meter of surface area, the standing crop in these North Carolina estuaries is one order of magnitude below that in embayments 3 to 10 m deep and two orders of magnitude below that in deeper embayments and on the continental shelf and slope. A linear relationship exists between the logarithms of volume of zooplankton per square meter and average length of the water column (Fig. 3) for all but the mid-ocean values (points 15–17). The correlation coefficient, 0.96, is significant at the 0.01 level. Conversion of the least squares regression

TABLE 3. Comparison of zooplankton volumes in area studied with those of other marine environments. Values followed by an asterisk are calculated from data in the reference.

Location	Mesh No. of net	Average depth m	Zooplankton volume			Reference
			ml/m³		ml/m²	
			Average	Range	Average	
Embayments						
1 Estuaries, N. C.	10	1.2	0.11	0.002–0.46	0.13	Present study
2 Lower Sheepscot Estuary, Maine	2	7	.38*	0–1.5	2.7	Stickney, 1959
3 Great Pond, Mass.	10	1	.14*	<.001–2.5	.14*	Barlow, 1955
4 Charlestown and Green Hill Ponds, R. I.	12	1	.67*	0–6	.67*	Conover, 1961
5 Block Island Sound	10	30	.68	.05–1.8	20	Deevey, 1952
6 Long Island Sound	10	20	.95	.1–6.2	19	Deevey, 1956
7 Delaware Bay	2	10	.3*	0–1.3	3.0*	Cronin et al., 1962
8 Biscayne Bay, Fla.	6	2	.16*	0*–1.5	.32*	Woodmansee, 1958
9 St. Andrews Bay, Fla.	10	3	.48*	.09*–0.91*	1.4*	Hopkins, 1966
Continental Shelf and Slope						
10 Gulf of Maine	0	140	.30*	.01*–1.5*	42	Redfield, 1941
11 Georges Bank	2	90	.72	.12*–1.7*	65*	Riley and Bumpus, 1946 (Deevey, 1952)
12 South of Long Island	6	60	1.07	.12–3.71	64*	Grice and Hart, 1962
13 South of Long Island	6	200[1]	.27	.04–0.76	54*	Grice and Hart, 1962
14 Cape Hatteras area	2	56[2]	.26*	.01–1.9	15*	St. John, 1958
Mid-ocean						
15 Sargasso Sea	6	4900[3]	.02	.01–0.04	4.0*	Grice and Hart, 1962
16 Sargasso Sea	2 and 8	2970[4]	.03	.01–0.21	38	Menzel and Ryther, 1961
17 Eastern Pacific	ca. 4	4000[5]	.08*	.01–0.40*	24	Blackburn, 1966a and b

[1] Upper 200 m sampled; average depth of water 700 m.

[2] Average depth sampled, 56 m; maximum depth sampled, 190 m; station depths range from about 10 to 3500 m.

[3] Upper 200 m sampled.

[4] Upper 2000 m sampled.

[5] Upper 300 m sampled.

of this relationship to antilogarithms yields:

$$\text{Zooplankton vol. (ml/m}^2) = 0.259 \times \text{avg length water column (m)}^{1.145}$$

The exponent, 1.145, is not significantly different from 1.000. Thus as a first approximation, the standing crop of zooplankton per square meter in areas less than about 100 m deep might be considered a linear function of depth. The average of the first 14 values for zooplankton volume per cubic meter in Table 3 is 0.46 ml/m³. Thus:

$$\text{Zooplankton vol. (ml/m}^2) \sim 0.5 \times \text{avg length water column (m)}$$

The presence of a small standing crop of zooplankton in the shallow estuaries we

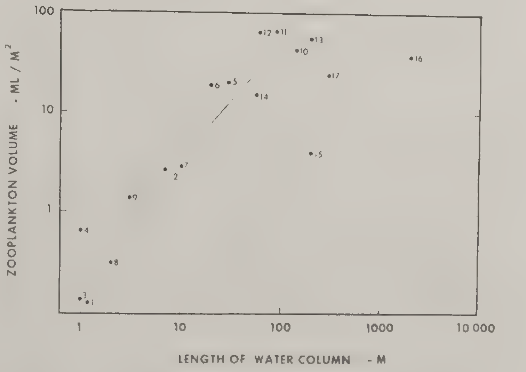

FIG. 3. Comparison of average zooplankton standing crop (per square meter) with average length of the water column sampled. The numbered points refer to locations in Table 3.

studied is thus in accord with the results of other investigations of coastal and estuarine areas (Fig. 3). The standing crops of zooplankton in the mid-ocean areas (points 15, 16, and 17 in Fig. 3) do not fit the regression. In two of the mid-ocean studies (points 15 and 17) only the surface layer was sampled, and the standing crop for the entire water column must have exceeded the values in Table 3; in the third (point 16), however, the sample was for the upper 2000 m of the Sargasso Sea and thus included all but a negligible fraction of the zooplankton.

Factors Controlling the Standing Crop of Zooplankton

Factors controlling the standing crop of zooplankton in North Carolina estuaries were not identified. In other studies the control of zooplankton abundance has been ascribed to low temperatures (Fish and Johnson, 1937; Riley, 1941), to inadequate food supply (Marshall et al., 1934; Menzel and Ryther, 1961), and to predation (Heinle, 1966). In the North Carolina estuaries standing crop was maximal during the coldest period, December through February, and had an inverse relationship with temperature. It was also unlikely that the high summer temperatures were unfavorable because Sutcliffe (1950) found zooplankton most abundant in the same area during July and August. The standing crop was also related inversely to the rate of net production of phytoplankton, both at the time of sampling and during the preceding survey, 5 weeks earlier (Table 4). Near the inlets maintenance of zooplankton at the same abundance as in the adjoining ocean might be achieved through tidal flushing and exchange. The standing crop per cubic meter near the inlets was not significantly different, however, from that at the heads of the estuaries.

Throughout our study the zooplankton population was so small in comparison with the available phytoplankton that multiplication of the zooplankton could not have been restricted by insufficient food, except perhaps during the winter when zooplankton was most abundant. The respiration and rate of feeding of the zooplankton were estimated roughly for each of our surveys (Table 4) by use of rates for *Acartia tonsa* (Anraku, 1964), the most common copepod in our study area (Sutcliffe, 1950). Anraku's results

TABLE 4. Standing crop and metabolism of zooplankton and phytoplankton. Phytoplankton data are taken from Williams (1966).

Survey	Water temperature C	Phytoplankton	Zooplankton						
		Net photosynthesis	Standing crop	Respiration		Filtering intensity	Phytoplankton available		Phytoplankton available/respiration
		mg C/m^2/day	mg C/m^2	mg C/m^2/day	% net Ps[1]	liter swept/m^3/day	mg C/m^2/day	% net Ps[1]	
Mar.	14	41	9.3	.70	1.7	27	2.2	5	3
Apr.	20	111	7.0	.60	.5	38	8.5	8	14
May	24	197	11.1	1.13	.6	74	14.7	8	13
June	28	273	11.7	1.37	.5	89	24.3	9	18
July–Aug.	26	310	3.3	.37	.1	23	7.2	2	19
Sept.	26	220	5.6	.63	.3	37	8.3	4	13
Oct.	17	118	5.2	.39	.3	19	4.5	4	12
Nov.	17	85	10.7	.92	1.1	45	7.7	9	8
Dec.	10	61	15.9	1.19	2.0	36	4.4	7	4
Jan.	7	56	28.7	1.84	3.3	31	3.4	6	2
Feb.	9	61	17.7	1.13	1.9	29	3.6	6	4
Average	18	139	11.5	.93	1.1	41	8.1	6	10

[1] Percentage net photosynthesis.

for *A. tonsa* from Massachusetts were interpolated and extrapolated as needed to cover our range of temperatures, and the zooplankton was assumed to have a respiratory quotient of 1.0. The values thus obtained for daily respiration of the zooplankton population ranged from 0.37 to 1.84 mg C/m^2 and represented a carbon demand of only 0.1 to 3.3% of the phytoplankton net photosynthesis. The percentage of the phytoplankton population potentially available each day to the zooplankton was obtained from the product of Anraku's values for milliliters swept clear per milligram of copepods and our estimates of zooplankton standing crop. This percentage ranged from 1.9 to 8.9% and averaged 4.1%. To estimate the quantity of phytoplankton carbon represented by these percentages we assumed that the algal cells divided once a day in warm weather (May through September) and once every two days in cool weather (October through April). This assumption is based on Curl and McLeod's (1961) observations on *Skeletonema,* an abundant phytoplankter in the Beaufort area (Williams and Murdoch, 1966). Thus, the estimated standing crop of algae equaled daily net photosynthesis in warm weather and was twice the daily net photosynthesis in cool weather. Our estimates of phytoplankton carbon potentially available to the zooplankton ranged from 2.2 to 24.3 mg C/m^2 and averaged 8.1 mg C/m^2. Potentially available phytoplankton carbon was 2 to 19 times the amount lost in zooplankton respiration, and thus during most of the year should not restrict growth and reproduction of the zooplankton. Use of a different respiratory quotient, such as 0.8, or of the respiratory and feeding rates for other copepod species would not radically alter our conclusions.

Zooplankton grazing should have minimal effect on the standing crop and production of phytoplankton, because the phytoplankton potentially available each day to the zooplankton was equivalent to only 5 to 9% of the net photosynthesis. Estimates of grazing intensity represented maximum values since some of the zooplankters may have been carnivores or detritus feeders. Estimates of potentially available carbon were minimal because the water contained abundant detritus from salt marshes and submerged grass beds.

Predation may be an important controlling factor. In warm weather, small fish were abundant in the estuaries. These fish, together with ctenophores and medusae, may consume enough zooplankton to hold it at the observed low concentration.

IMPORTANCE OF THE ZOOPLANKTON

Analysis of our data thus suggests that zooplankton is relatively unimportant in the food chains of the shallow area we studied, even though it may be turning over rapidly due to the combination of heavy predation and abundant food (Heinle, 1966). Throughout the year zooplankton remained so sparse that it could not have consumed more than a small fraction of the available phytoplankton production which, in turn, is only a fraction of the total plant production. The net phytoplankton production, 53 g C/m^2/year, is similar to that in the open sea, although vertically concentrated in embayments averaging only 1.2 m deep. This plentiful and concentrated plant production supports an abundance of benthic animals (Brett, 1963) which doubtless contribute most of the herbivore link in the food chain. Despite the concentrated food supply, holoplanktonic animals are less abundant per unit of water volume than in neritic areas along the Atlantic Coast of the United States.

This dearth of zooplankton relative to the available plant production may be normal for shallow embayments and, as Raymont (1966) has suggested, the grazing of zooplankton may have little effect on the density of algae in such areas. We compared the ratio of annual phytoplankton net production to average standing crop of zooplankton with the average depth of the water for seven areas ranging from shallow salt ponds, to the open sea (Fig. 4). For two areas, Charlestown and Green Hill Ponds, Rhode Island, and St. Andrews Bay, Florida, gross photosynthe-

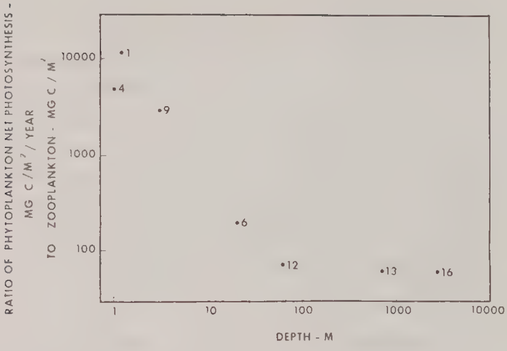

Fig. 4. Comparison of the ratio of annual phytoplankton net photosynthesis to average zooplankton standing crop with the average depth of the water. The numbered points refer to locations in Table 3.

sis was estimated from data on chlorophyll, temperature, and transparency by using relationships obtained previously for shallow embayments (Williams, 1966; Williams and Murdoch, 1966), and net photosynthesis was assumed to be one-half of gross photosynthesis. The three values for offshore areas (Ryther, 1963) were used as measurements of net photosynthesis although they were obtained by the C^{14} technique and may represent some quantity between net and gross photosynthesis (Strickland, 1960). For studies containing no data on the ratio of displacement volume to dry weight of zooplankton, an average value of 90 mg/ml was used. The carbon content of zooplankton was assumed to be 40% of the dry weight (Curl, 1962; Beers, 1966). The ratios of phytoplankton production to zooplankton standing crop thus obtained range from 11,800 in the area we studied to 60 in the Sargasso Sea. The relationship between the ratios and water depth (Fig. 4) suggests that zooplankton may achieve maximum importance in the consumption of phytoplankton in waters deeper than about 100 m, and become steadily less important with decreasing depth in areas shallower than 100 m.

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Notes on the Habitat and Anatomy of *Jouannetia quillingi* from North Carolina Coastal Waters

BY

DOUGLAS A. WOLFE

Notes on the Habitat and Anatomy of *Jouannetia quillingi* from North Carolina Coastal Waters

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DOUGLAS A. WOLFE

Bureau of Commercial Fisheries, Radiobiological Laboratory
Beaufort, North Carolina 28516

(Plate 15; 1 Textfigure)

Jouannetia quillingi IS A RARE BIVALVE which I have recently discovered burrowed into pieces of marl and sandstone submerged in coastal waters near Beaufort, North Carolina. Before describing *Jouannetia (Pholadopsis) quillingi* (Pholadidae; Jouannetiinae) as a new species, TURNER (1955) examined (among others) 2 specimens collected in 1885 on the *Albatross* cruises southeast of Cape Fear, North Carolina. The specimens came from depths of 17 and 18 fathoms, but no records were available on whether the specimens were living or dead, or on the substratum in which they were found. Specimens of *J. quillingi* are rare, and the species has not been reported from elsewhere off North Carolina, even though several faunal surveys have been conducted in the area (CERAME-VIVAS & GRAY, 1966; MENZIES *et al.*, 1966; WELLS, WELLS, & GRAY, 1964; PEARSE & WILLIAMS, 1951). The soft parts of this species were heretofore unknown.

Throughout 1966 and in early 1967, several boats from Beaufort, North Carolina, regularly trawled for calico scallops in 10 to 15 fathoms just south of Beaufort Inlet and west of Cape Lookout (approximately 34°20-32′ N; 76°35-55′ W). The bottom in this area consists mainly of sand and shell fragments, but large pieces of Trent marl, coquina and coral *(Siderastea elegans)* were encountered occasionally in the trawls. I periodically met the trawlers at the dock to collect specimens from the catch as it was unloaded. On January 23, 1967, I found several large pieces of Trent marl which had been dumped beside the dock after the previous day's work. Nine dead, but otherwise intact, specimens of *Jouannetia quillingi* were retrieved from their tight burrows in one piece (about 10 in. x 7 in. x 2½ in.); 2 others in the same rock were discarded because they were badly damaged. No more specimens were found in other similar pieces of rock in the same pile. The clams had been out of the water at least 27 hours, but no more than 36 hours; the tissues were still quite moist, but were probably in early stages of decomposition. Seven of the 9 specimens were preserved in 40% methanol containing 0.1 molar Na_2CO_3; the others were cleaned and dried, one *in situ* in its burrow (No. 1253; Plate 15, Figure 1 a). Other specimens (about 20 in all) were collected from burrows in similar rocks trawled from the same area on January 17, March 2, March 3, and May 12, 1967 (No. 1544; Plate 15, Figure 1 b), but only one of these (No. 1366; March 2, 1967) contained the soft parts; it was preserved as described above. Several small immature specimens were also included in the March 2 sample. A representative selection of immature and adult specimens, including the one illustrated in Plate 15, Figure 1 b, now is in the collection at the Museum of Comparative Zoology, Harvard University.

HABITAT AND ECOLOGY

Substratum: All specimens of *Jouannetia quillingi* were burrowed into the tops or sides of pieces of soft rock obtained from depths of 10 to 15 fathoms. The rock usually was marl (limestone) from the Trent Formation, which outcrops at several points along the continental margin of the Carolinas (PEARSE & WILLAMS, 1951). In one such piece of marl, recent burrows and shells of *J. quillingi* were found among a concentration of lower Miocene fossil casts of *Venus gardneri* KELLUM. On March 3, 1967, *J. quillingi* were found in a softer piece of rock (Plate 15, Figure 2), which seemingly consisted of cemented sand grains, more nearly characteristic of the formations of coquina in this area (WELLS & RICHARDS, 1962; MENZIES *et al.*, 1966). The shell of *J. quillingi* completely fills the lower part of the burrow, and the callum of the left valve in the adult is loosely cemented against the bottom and sides of the burrow so that only the right valve is free to move (Plate 15, Figure 1). The callum, which is so extensive in the non-burrowing adult, is completely lacking in young burrowing specimens. *Jouannetia,* like other callum-building pholads (Turner, 1954), probably extends its foot through the anterior gape of the shell while burrowing, but when burrowing ceases, the callum is built and the foot is resorbed. The siphons must be extended a few millimeters behind the siphonoplax to reach the narrow (2 to 4 mm diameter) aperture of the burrow (Plate 15, Figure 2). The entrances to the burrows are extremely inconspicuous from the outside; the posterior end of the siphonoplax of the entrenched mollusk is generally not visible through the aperture. *Jouannetia quillingi*'s apparent preference

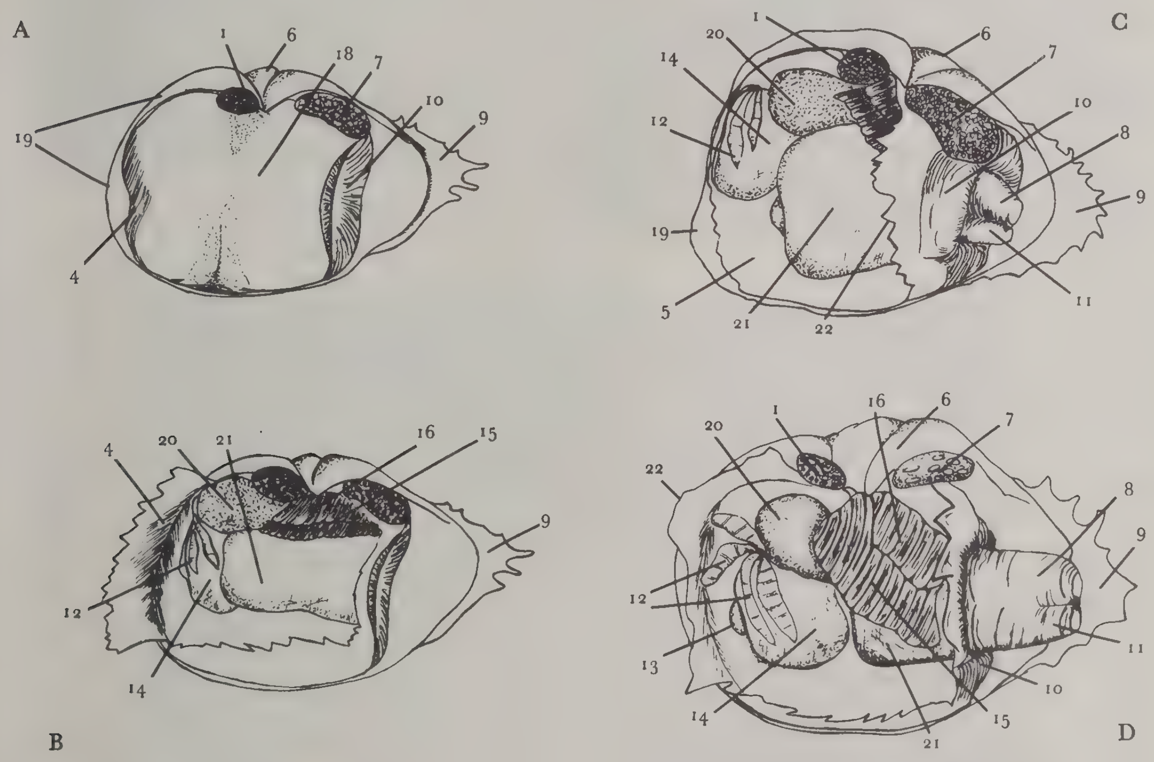

Figure 1

Internal morphology of *Jouannetia quillingi*

A: Specimen collected January 23, 1967, with left valve removed. B: Same specimen, with left mantle laid back. C: Different specimen from same sample, left mantle laid back. D: Specimen collected March 2, left mantle laid back.

Explanations of numbers (after Turner, 1962)

1. Anterior adductor muscle
4. Thickened anterior margin of mantle
5. Mantle
6. Shell
7. Posterior adductor muscle
8. Excurrent siphon
9. Siphonoplax
10. Siphonal retractor muscle
11. Incurrent siphon
12. Labial palps
13. Foot
14. Visceral mass (abdominal mass of Fischer, 1860, 1862)
15. Inner demibranch of gill
16. Outer demibranch of gill
18. Closed mantle of adult
19. Edge of calcareous callum
20. Brownish digestive tissue
21. Retracted siphons
22. Cut edge of mantle

for substrata of soft rock is characteristic of other species of the genus, although the holotype of *J. quillingi* was reportedly found in submerged and rotted wood (Turner, 1955).

Associated Mollusks: Principal mollusks found in conjunction with *Jouannetia quillingi* on and in similar pieces of rock taken in hauls made for calico scallops are listed below:

GASTROPODA

Vermicularia spirata Philippi, 1836
Vermicularia knorri (Deshayes, 1843)

PELECYPODA

Lithophaga bisulcata (Orbigny, 1842)
Lithophaga aristata (Dillwyn, 1817)
Gastrochaena hians Gmelin, 1791
Gastrochaena ovata Sowerby, 1834
Petricola typica (Jonas, 1844)
Hiatella arctica (Linnaeus, 1767)
Pododesmus rudis (Broderip, 1834)
Diplodonta punctata (Say, 1822)
Chama macerophylla Gmelin, 1791
Chama congregata Conrad, 1833
Pseudochama radians (Lamarck, 1819)
Arca imbricata Bruguière, 1789

ANATOMY of *Jouannetia quillingi*

Three preserved specimens were dissected: two from the January sample and the one collected on March 2. The tissues of the former specimens were very soft and disintegrated upon extensive probing, and the tissues in the latter were distinguished much more readily. General internal morphology of all 3 specimens is shown in Text figure 1. For convenience, the numbers identifying anatomical features are the same, where possible, as those used by Turner (1962).

Upon removing the left valve with its overlapping callum, one sees only the adductor muscles and the closed mantle of the organism (Text figure 1 A). The mantle is thickened along the anterior margin and also posteriorly where it joins the siphonal retractor muscles. In the 3 specimens dissected, the siphons were fixed in different positions, ranging from fully extended (Text figure 1 D) to completely retracted (Text figure 1 B). The siphons are of equal length and are covered with a rather heavy brown periostracal sheath.

When the mantle is opened and laid aside (Text figures 1 A to 1 D), the most prominent anatomical feature is the large, white, smooth, rounded body of the retracted siphons (No. 21). When the siphons are fully retracted (Text figure 1 A, 1 B), they occupy most of the space enclosed by the mantle and thereby displace the visceral mass anteriorly and dorsally. The visceral mass is differentiated into a cream-colored ventral portion (No. 14) and a more dorsal brownish digestive gland which was greenish in the March 2 specimen (No. 20). The paired labial palps are long and strap-like and lie on either side of the slit-like mouth on the antero-dorsal surface of the cream-colored portion of the visceral mass. The labial palps were overlooked during the dissection of the first 2 specimens because of the condition of the tissues, but I have included them in their proper position in Text figures 1 B and 1 C. The 2 paired demibranchs of the gill are situated mainly dorsal and posterior to the visceral mass and the retracted siphons.

The anatomy of *Jouannetia quillingi* differs somewhat from that of *J. cumingi* and *J. globulosa* as illustrated by Fischer, 1860, 1862). [Fischer's original drawings are reproduced in part by Turner, 1962.] Fischer pictures the siphons of both *J. cumingi* and *J. globulosa* as being very much shorter than those of *J. quillingi*, so that the mantle cavity is occupied by only the visceral mass, labial palps, and gills. Fischer also does not mention any differentiation of the visceral mass, a feature quite noticeable in my 3 dissections of *J. quillingi*. According to Turner (1954, 1962), a detailed description of the anatomy of *J. cumingi* Sowerby is given also in a private publication by Egger (1887), but I have been unable to examine this reference.

SUMMARY

Jouannetia quillingi Turner, 1955, first found off the coast of North Carolina during the *Albatross* cruises of

Explanation of Plate 15

Jouannetia quillingi from 10 to 15 fathoms off Beaufort, North Carolina

Figure 1 a: Dorsal view of specimen *in situ* in shallow burrow in Trent marl. The original entrance of the burrow was destroyed during removal of excess rock.

Figure 1 b: View of left valve of deeply embedded specimen. The upper one-half of the burrow has been removed.

Figure 2: Typical burrow of *Jouannetia quillingi* in soft cemented sandstone, sectioned to show the shape and proportions of the burrow.

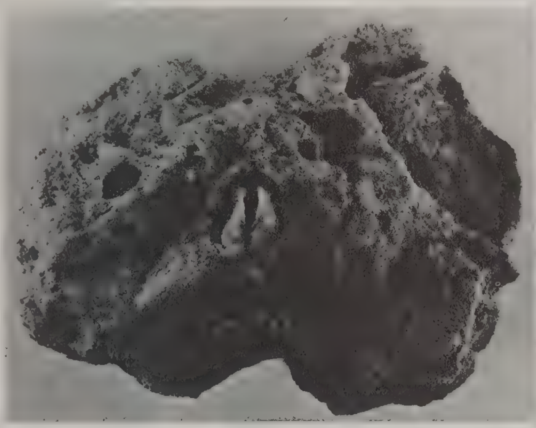

Figure 1 a

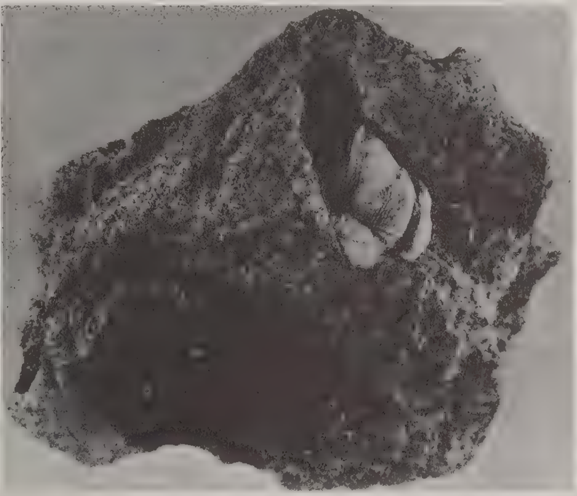

Figure 1 b

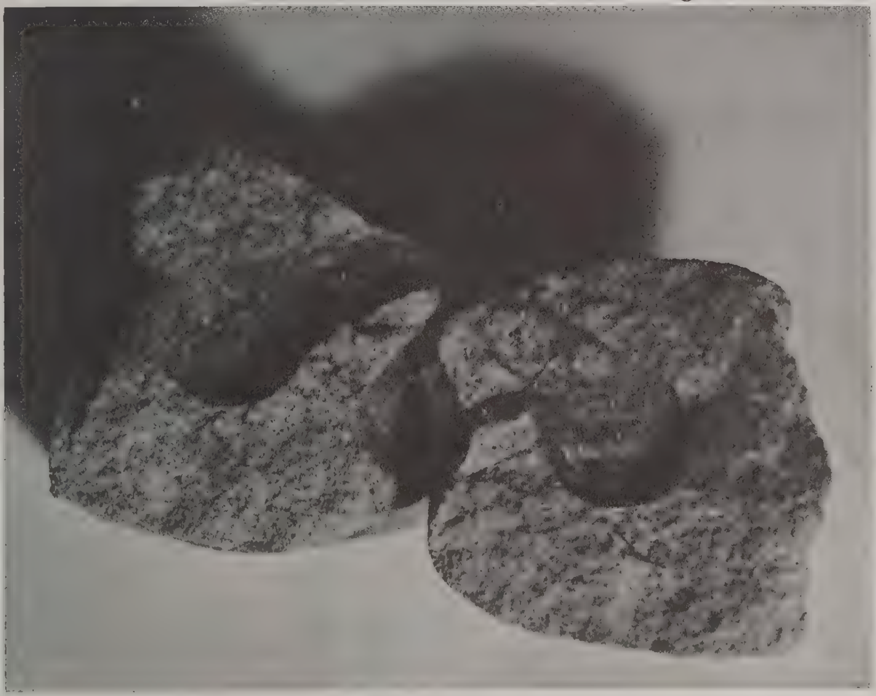

Figure 2

1885, has been rediscovered south of Beaufort Inlet in 10 to 15 fathoms. The species lives burrowed into soft marl and sandstone. It seems likely that the rarity ascribed to the species arises at least partly from the seclusion afforded by its inconspicuous burrows in submerged rock. The general internal morphology of the species, heretofore unknown, has been described.

ACKNOWLEDGMENTS

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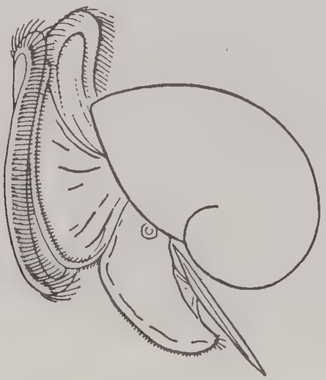

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A COLONY OF *EUGLANDINA ROSEA* AT BEAUFORT, NORTH CAROLINA

DOUGLAS A. WOLFE AND JERALDINE H. BROOKS

Bureau of Commercial Fisheries
Radiobiological Laboratory[1]
Beaufort, North Carolina 28516

The range of the carnivorous land snail *Euglandina rosea* (Férussac) was reported by Pilsbry (1946) to extend from the vicinity of Yemassee, South Carolina, along the coastal plain south and west into Louisiana, including all of Florida. Burch (1962) gave the range as South Carolina, Florida, Alabama, Mississippi, and Louisiana. The northernmost record is Charleston, South Carolina (Mazÿck 1913). The present report concerns a colony of living *Euglandina rosea* at Beaufort, North Carolina, some 260 miles north and east of Mazÿck's Charleston record.

On March 1, 1968, we found nine live specimens of *E. rosea* along the north side of Highway 70 at the extreme western edge of Beaufort. The snails were crawling within the perimeters of two adjacent old foundations from which buildings had been moved 2 or 3 days earlier. Nine additional shells of *E. rosea* were found at the same time and place; eight contained intact dead snails and the other was empty. We speculate that these specimens might have died because of the abrupt exposure to the cold wind blowing at the time (about 2° C; 25 m.p.h.).

Three other gastropod species were abundant at the collecting site: a slug, *Limax flavus* Linné, and two snails, *Triodopsis hopetonensis* (Shuttleworth) and *Helicella caperata* (Montagu). Whereas most of the shells of *Triodopsis* and *Helicella* were empty, living slugs were under and around nearly every piece of rubble moved (boards, tin cans, and cement blocks). We tested these and other gastropods as food sources for *Euglandina* as follows. Three large *E. rosea* were confined in a 1-gallon jar with seven *Limax flavus*, one *Triodopsis albolabris* (Say), and one *Mesomphix rugeli* (Binney). *Euglandina* occasionally attacked the slugs but they responded immediately with a hasty retreat and the carnivore never pressed the attack. After 3 days, three *Triodopsis hopetonensis* were added to the jar. Between the fifth and sixth days, the three *Euglandina* consumed all the animals except the slugs. After the sixth day, the seven slugs were removed unscathed. Four *Helicella caperata* were introduced on the morning of the tenth day; one was consumed within 24 hours, two more after 24 hours, and the last after 31 hours. Thus, this localized colony of *E. rosea* was apparently surviving on *Triodopsis hopetonensis* and *Helicella caperata* and probably not on the slugs. We did not notice any particular food preference; all four species of snails offered were eaten. Feeding was usually at night. Ingram and Heming (1942) reported that a single captive *E. rosea* had selected only *Mesomphix inornatus* and *Anguispira alternata* from a variety of snails offered, including *Triodopsis albolabris*.

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[1] The Radiobiological Laboratory is jointly supported by the Bureau of Commercial Fisheries and the Atomic Energy Commission.

Although the range of *Euglandina rosea* obviously extends as far north as Beaufort, North Carolina, its distribution must be discontinuous and confined to small colonies occurring here and there. A single dead specimen, reportedly found in a yard on the east side of Beaufort, came to the attention of one of the authors (DAW) during the summer of 1967, but an intensive search of the adjoining area failed to reveal additional specimens. Perhaps *E. rosea* can survive the North Carolina winters only with the protection afforded by buildings or other similar cover.

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Functional Significance of the High Zinc Content of Crassostrea virginica, Douglas A. Wolfe, Jo-Ann M. Lewis and Jeraldine H. Brooks, Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, N. C. 28516

Levels of zinc in oyster tissues generally exceed those in sea water several thousandfold. The concentration of zinc by oysters is of radioecological significance because zinc-65 sometimes occurs in fallout and in reactor effluents. To characterize the physiological role of zinc in oysters, we have studied the interaction between zinc and oyster proteins *in vitro*. Upon gel filtration of the extracellular fluid of oysters, about 97 percent of the total zinc is eluted with the high molecular weight proteins. Prolonged dialysis at pH 8, however, removed up to 95 percent of the zinc in buffered extracts of whole oysters; continued dialysis against repeated changes of buffer did not remove the remaining zinc. Although zinc is required for enzymatic activity of alkaline phosphatase in oysters, the alkaline phosphatase in the extracts was only slightly inhibited by this treatment. These data suggest that most of the zinc associated with soluble oyster proteins is not required metabolically.

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Growth of *Rangia cuneata* Gray[1]

Douglas A. Wolfe
Ernest N. Petteway[2]
Bureau of Commercial Fisheries
Radiobiological Laboratory
Beaufort, North Carolina 28516

ABSTRACT: A standing population of *Rangia cuneata* Gray was sampled at one station on the Trent River (Neuse River watershed; eastern North Carolina) 12 times between November 9, 1965, and July 6, 1967. Length-frequency analysis of the clams revealed five distinct size groups, which were recognizable in three or more consecutive samples. From the progression of lengths in the size groups, two growth parameters were estimated in order to construct hypothetical von Bertalanffy curves describing growth in *Rangia cuneata*. The derived growth equations indicate that the clam reaches its maximum length of about 75 mm in approximately 10 years.

Introduction

Rangia cuneata (Gray) (Pelecypoda: Mactridae) occurs in brackish water situations from the Chesapeake Bay to Texas, and is harvested commercially to a limited extent from estuarine areas along the North Carolina coast. Although *Rangia* is of potential commercial importance throughout its range, very little is known about the growth or general life history of the species. Fairbanks (1963) suggested that in Louisiana *Rangia* spawns during spring (March–May), and again, but less intensively, from late summer into November. Autumnal spawning was confirmed by Pfitzenmeyer and Drobeck (1964), who found mature gametes in *Rangia* from the Potomac River, Maryland, in late August. From analysis of growth lines, Fairbanks (1963) inferred average annual size increments through the first 3 years of growth. The average shell length of 3-year-old clams was in the range of 24–34 mm. In the Potomac population, clams 35 to 45 mm long were believed to be 4 years old (Pfitzenmeyer and Drobeck, 1964). No additional information on growth of *Rangia* in natural populations is available in the literature. We had an opportunity to evaluate growth of *Rangia cuneata* from samples which were originally collected for a radioecological study of fallout from nuclear weapons tests (Wolfe, 1967; Wolfe and Schelske, In press).

Sampling Methods and Ecology of the Sampling Station

Samples of *Rangia cuneata* were collected by raking near the shore of the Trent River at the junction of Wilson Creek (Wolfe, 1967). The prongs on the clam rakes were 20 to 25 mm apart; clams shorter than 30 mm were therefore not sampled reliably. Collections were made at irregular intervals (usually once every 4–6 weeks) from November 9, 1965, to July 6, 1967. Although the total bottom area from which collections were made was only about 500 m^2 (10 × 50 m), the population was not depleted by removal of ½ to ¾ bushel of clams per sample. The 12 samples contained from 129 to 1,297 animals each, with a mean of 524.

At each sampling, salinity and water temperature were measured with an electrodeless induction salinometer. Salinity measurements, which ranged from 0.01‰

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[2] Present address: Department of Zoology, University of North Carolina, Chapel Hill, N.C.

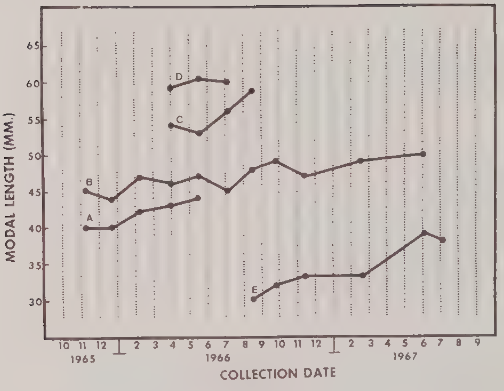

Fig. 1. Progression of modal lengths from length frequency analysis of 12 *Rangia* samples. Lines A-E represent the five peak size groups which were traceable through three or more consecutive samples.

TABLE 1. Results of Diaz and Ford-Walford plots.[1]

Method	Time interval (mo)	a (mm)	k (mo^{-1})
Diaz	Irregular	--	−0.0033
Diaz	1	94.00	0.0109
Diaz	3	66.36	0.0229
Ford-Walford	1	78.09	0.0161
Ford-Walford	3	64.03	0.0272
Means (of four results)		75.62	0.0193

[1] All but the first Diaz method used points of intersection between length progressions and monthly grid from Fig. 1.

(March 29, 1966) to 6.0‰ (December 20, 1965), showed a seasonal variation from freshwater in the spring and summer to brackish water in the late fall and early winter. The lower salinities in this range apparently constituted a barrier to *Rangia* because the clams were absent about 2 miles farther upstream. The water temperatures measured at Wilson Creek ranged from 4.8 C (February 28, 1966) to 34.7 C (July 5, 1966). Other molluscs encountered with *Rangia* at Wilson Creek included *Polymesoda caroliniana* (Bosc), *Congeria leucophaeta* (Conrad), and rarely *Anodonta imbecilis* Say.

Analysis of Growth in *Rangia*

The left valve from each clam was measured with a ruler to the nearest millimeter, and the percentage frequency of every length was calculated for each sample of clams. The percentage frequencies were then graphed versus length for each sample. To emphasize central tendencies, the plots were smoothed by a moving average of three intervals, giving the center value double weight (Diaz, 1963). The samples usually consisted of more than one size class, as indicated by the presence of several peaks on the length frequency graphs. Only five distinct peaks could be traced through three or more consecutive samples. The progressions of the modal lengths of these five peaks, shown in Fig. 1, were used to construct a hypothetical von Bertalanffy growth curve for *Rangia cuneata*.

The von Bertalanffy growth curve is a decaying exponential that has been used to describe growth in a variety of forms (von Bertalanffy, 1938; Beverton and Holt, 1957; Fabens 1965). The animal's length L at any age t can be expressed as:

$$L = a(1 - be^{-kt})$$

where a, b, and k are parameters characteristic of the particular animal or population. The theoretical maximum length is equal to a and is approached asymptotically as t increases. The parameter b is the ratio of total lifetime growth (after birth, or, in bivalve molluscs, after settling) to total length, or:

$$b = \frac{a - c}{a}$$

where c is the average length of the clam shell when the larvae settle (t equals to zero). Determination of b obviously requires knowing the length at time zero. The exponential k is related to the catabolic rate of the animal. Two parameters, a and k, can "easily be determined from data only on sizes at known time differences, with no knowledge of absolute age" (Fabens, 1965). These size data are provided by the progressions of modal lengths in Fig. 1. The data were manipulated by two methods for estimation of a and k: (1) Diaz increment technique (Diaz 1963, 1966; Gulland and Holt 1959), and (2) Ford-Walford technique (Walford 1946, Hancock 1965). The resultant values for a and k are shown in Table 1.

In the Diaz increment technique, the change in length per unit time, $\Delta l/\Delta t$, is graphed against the average length during the time interval, $\bar{l}$. A straight line, fitted to the plot by least squares, will have a slope of $-k$ and an intercept ka. Application of this technique to the modal lengths at our irregular sampling times produced a nonsense result (Table 1). We therefore superimposed on the original data a monthly grid (Fig. 1) and applied the Diaz technique to data derived from points of intersection between the modal progressions and the grid. Growth parameters were determined for 1-month and 3-month intervals between data points (Table 1).

In the Ford-Walford technique, the length at any age, l_t, is graphed against the length after a specified time, l_{t+1}. The time interval may be arbitrary but must be the same between all values of l_t and l_{t+1}. A straight line fitted to the points will have a slope of e^{-k} and an intercept of $a(1 - e^{-k})$. Since the time interval must be standardized for this technique, Ford-Walford plots were made by using the intersects between lines of progression and the grid in Fig. 1, again at both 1- and 3-month intervals (Table 1).

A von Bertalanffy growth curve was constructed from the mean values for a and k (Table 1) by assuming the length at $t = 0$ to be 0.375 mm, which is the approximate length of *Rangia cuneata* at the time of larval settling (Fairbanks, 1963). Thus b is $(75.62 - 0.375)/75.62$ or 0.995. Chanley (1965) found the length of metamorphosing *Rangia* larvae to be about 0.175 mm, which would increase the value of b to 0.998. The von Bertalanffy curve derived is shown in Fig. 2. The original data points were fitted on the same graph by assuming that all larval settling occurs on October 1 (from a late summer spawn), and by connecting successively longer modal groups by the shortest possible time, based on calendar months. Although this approach is arbitrary, the closeness of the fit might merit some interest.

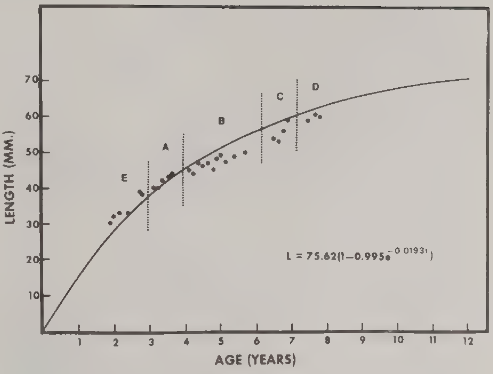

Fig. 2. Theoretical growth of *Rangia cuneata* Gray, expressed by von Bertalanffy growth curve with mean values of a and k (Table 1). Points are modal lengths of size groups A-E from Fig. 1, fitted to the curve as explained in the text.

Table 2. Predicted and reported length (mm) of *Rangia cuneata* at different ages.

Age (years)	Predicted from von Bertalanaffy equation	Fairbanks (1963)	Pfitzenmeyer and Drobeck (1964)
0	0.375	0.375	—
1	16.0	15–20	—
2	28.3	20–29	—
3	38.0	24–34	—
4	45.8	—	35–45

Predictions of growth from the curve in Fig. 2 correspond well to size and age estimates for *Rangia* from Fairbanks (1963) and Pfitzenmeyer and Drobeck (1964) (Table 2). The predicted maximum length, $a = 75.62$ mm, is also compatible with our observations on *Rangia* in the field. Clams over 70 mm long are rare. Of the 6,287 clams measured for this study, only 7 exceeded 70 mm, and the maximum length was 73 mm. The largest specimen recorded in any of our previous samples was 81 mm long and was collected in the Neuse River near Lewis Ferry (Wolfe, 1967). Thus, despite the limited length frequency data upon which this study was based, the von Bertalanffy equations derived from these data appear valid for estimating growth of *Rangia cuneata*.

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SAFE LEVELS OF RADIOACTIVITY IN AQUATIC ENVIRONMENTS

As nuclear energy supplies ever-expanding proportions of man's power requirements, the dose of background radiation to man from his environment will increase. The continuous disposal of radioactive wastes into aquatic environments should be evaluated on the basis of long-term population effects from chronic exposure to low-level radiation. In this article, we discuss the implications of radioactive waste disposal into aquatic environments, and consider those aspects of radiation physiology, radioecology and health physics used in developing standards for the adequate protection of aquatic ecosystems and man from excessive doses of radiation.

INTRODUCTION. — The rapidly expanding use of nuclear fission for power production and desalination has resulted in widespread introduction of radioactive materials into aquatic environments. Once radioactivity enters the environment, only physical decay can eliminate it. We are therefore faced with the problem of disposing of radioactive wastes in a manner that will not endanger the future use of our environment. In this paper we examine the techniques applied to the protection of aquatic environments from undue radioactive contamination which might adversely affect the availability of any food resource or subject man to unhealthful radiation doses.

Two general approaches have dominated the disposal of radioactive wastes. Highly radioactive materials usually are concentrated to a minimum volume, then packaged in a semi-permanent shielded container and stored in a place far removed from human activity. This is the principle behind storage of radioactive wastes in underground tanks, in thin cement grouting layers in deep rock strata, and in concrete packages at the bottom of the oceans (International Atomic Energy Agency 1965, National Committee on Radiation Protection 1954a, Struxness In Press). In this paper we focus on the second concept of waste disposal, in which low-level radioactive wastes are diluted and dispersed directly into the environment.

The primary source of environmental contamination to date has been fallout from atomic test explosions, but the relative contribution from this activity is expected to continue to diminish in the future. Instead, wastes will arise from increased use of radioisotopes in clinical and experimental research applications and, principally, from the use of nuclear reactors in power plants and ships, including submarines. During typical reactor operations, fission products are not released, but occasionally a fuel element may rupture and leak into the cooling water. Additional radionuclides, however, are induced in the coolant water as it passes through the regions of high neutron-flux within the reactor, and this induced radioactivity is expelled intermittently from the reactor. This problem of disposal is especially urgent on a nuclear submarine where little space is reserved for storage of wastes. Another potential source of radioactivity in the environment is from the use of nuclear explosions for excavation, as in canal or harbor construction. Underlying any additions of artificial radionuclides to the environment must be the premise that life, including man, can safely tolerate a limited but sustained increase in radiation from the environment.

This premise undergoes continuous scrutiny from certain scientific bodies which were established for the express purpose of evaluating effects of radiation on biological systems, and especially on human beings. These scientific bodies include the International Commission on Radiological Protection (ICRP), sponsored under the International Society of Radiology; the U. S. National Committee on Radiation Protection and Measurements (NCRP); the Committees on the Biological Effects of Atomic Radiation, under auspices of the National Academy of Sciences—National Research Council; the United Nations' Scientific Committee on the Effects of Atomic Radiation; and the Federal (U.S.) Radiation Council (FRC), which was designed to provide governmental policy on human radiation exposure. Other nations also have governmental agencies with functions similar to those of the FRC. As suggested by this listing of national and international scientific bodies, the protection of human beings from overexposure to atomic radiation is of vital concern. The problems in determining what amount of radiation constitutes overexposure are manifold and imposing. The earlier committees, especially the ICRP and NCRP, were initially concerned with the protection of radiation workers, and have therefore recommended limits for occupational exposure to radiation, both from internal (NCRP 1959, ICRP 1960) and external sources. These recommendations were designed to protect an individual during his normal life-span from adverse effects of radiation.

With the advent of environmental contamination by wastes from the worldwide use of nuclear fission for power, our primary concern should perhaps shift from the radiological protection of individuals to protecting the genetic stability of the entire world population. Whereas an adult individual can tolerate safely 5 rems (r) per year (NCRP 1954b, 1959; ICRP 1960), it has been estimated that a dose of only 30-80 r, accumulated by the gonads, might double present mutation rates with uncertain consequences to the population (NAS-NRC 1956). For this reason, scientific committees on radiological protection have more recently re-evaluated in terms of genetic effects the premise that a sustained increase in environmental radiation is safe.

Let us now examine that premise and then consider the additional information required for establishing those « limits of safety » for radioactivity in our surroundings, especially as applied to aquatic environments.

HUMAN RADIATION TOLERANCE. — Although life began, and species evolved, in the presence of radiation—radiation from cosmic sources and from naturally occurring radioisotopes such as radium, carbon 14, and potassium 40—geneticists are almost unanimous in the view that any ionizing radiation is genetically undesirable. For example, Grosch (1965) states « Some natural radiation is unnecessary and may be potentially harmful. Included in this category are cosmic rays, body burdens of C^{14} and K^{40}, and the gamma radiation from earth, rock and the structural materials of our buildings ». The natural radioactivity from these sources obviously cannot easily be avoided and must be accepted as a normal hazard of living. The level of background radiation depends on altitude (elevation), latitude, and type of rock strata, and the dose may vary from 53 mr/year (to an individual on the open ocean at the equator) to 560 mr/year (at 55° N latitude, 20,000-foot elevation, on granitic strata) (Libby 1955, Kinsman 1958). A reasonable average dose is 140-150 mr/year. Since people have lived under similar circumstances of natural selection for several generations in areas differing by 150 mr, or more, per year in dose of natural radiation it is probable that an increase of 150 mr/year would constitute no threat to the genetic stability of human populations. We cannot say that an increased dose of 150 mr/year is the limit of safety, or even that it approaches that limit, but we can state with some confidence that an additional 150 mr/year would not be genetically critical. Such an increase would result in an additional 4.5 r accumulated dose to the gonads at age 30, the average parental age at the birth of any child in the U. S.; and 6.75 r at age 45, when reproduction more or less ceases. It is significant that the limits recommended elsewhere generally approximate this dose (Table 1).

TABLE 1

Recommended Limitations on Radiation Dose to General Population

Source of recommendation	Accumulated whole body dose at age 30 (rems)
ICRP (1959, 1960, 1966)	5[a]
NCRP (1954b, 1959)	14[b]
NAS-NRC (1956, 1960)	10[c]
FRC (1960)	5[a]

[a] Exclusive of background and medical exposure.
[b] From all sources, including background and medical dosages, averaged for 10^6 population.
[c] Exclusive of background, but including medical exposure.

We have considered in the foregoing discussion the levels of radiation which can be safely tolerated genetically by the general population. If only limited portions of a population are exposed, then greater doses can be withstood with no significant genetic effects to the whole population. Individual adults can tolerate much higher doses because the radiation-sensitive genetic material is no longer of prime consideration. The committees on radiation safety instead consider certain somatic effects, such as leukemia, or shortening of life-span, which might appear at some time following a latent period after exposure to radiation. The recommendations made by ICRP, NCRP, and FRC for maximum exposure of individuals working with radioactivity are identical: that occupational exposure will not exceed a whole body (or gonadal) dose of 3 rems during any period of 13 weeks, and that the accumulated dose at age N years shall not exceed 5 (N-18) rems, or in other words, 5 rems per year after age 18 (when occupational exposure might start). This limit of 5 rem/year is based upon exposure of whole body. Less sensitive portions of the body, especially if not significantly involved in blood formation, can tolerate still higher doses. For example, the dose permitted (NCRP 1959) for the hands, forearms, feet, and ankles is 75 rems/year. The ICRP (1960) also specified two alternate standards: a maximum dose of 1.5 rem/year for non-radiation workers who work near or occasionally visit controlled areas; and a maximum dose of 0.5 rems/year for the general public living in the neighborhood of a controlled area. These standards for different segments of the population are summarized in Table 2.

TABLE 2

Recommended Maximum Permissible Annual Doses of Radiation for People in Different Exposure Categories (ICRP 1959, 1960, 1966)

Group exposed	Maximum permissible dose per year (rems)[a]	Relative dose
General population	0.17	1
Communities in vicinity of controlled areas	0.5	3
Occasional visitors to controlled areas	1.5	9
Radiation workers	5.0	30

[a] All specified limits are for total whole body dose from both internal and external sources, exclusive of background and medical exposure.

STANDARDS APPLICABLE FOR GENERAL ENVIRONMENTAL CONTAMINATION. — The question now arises as to which set of standards should be applied to the control of waste disposal, and we might answer quickly that all should be used—each for its intended application.

This approach is certainly valid, now, while nuclear reactors are still relatively scarce, and significant doses may be encountered only in very limited areas in the immediate vicinity of nuclear operations. When a power company plans to build a nuclear power station near the Atlantic Coast in northeastern United States, it need not be concerned about the effects of its radioactive effluent on the genetic stability of the world population, or even of the population of northeastern United States. There would be no such effects at this time. It is likely, however, that the power company would already need to consider whether its anticipated effluent wastes will significantly affect food and water resources of communities living near the proposed reactor site. It requires little foresight, therefore, to become concerned about eventual levels of environmental radioactivity from the mushrooming expansion of peaceful uses of atomic energy.

If nuclear energy is used to supplement the rapidly decreasing supply of fossil fuel, and also to convert sea water to satisfy our increasing demands for fresh water, we can anticipate a gradual increase in environmental radioactivity during the next several centuries. This increase will become more pronounced as presently underdeveloped nations become more industrialized. As the use of nuclear power becomes more and more widespread, the concern must eventually be expressed for the general population. Since industrial pollution is more easily controlled during its initial phases, instead of after some unacceptable level has been established, it seems reasonable to think now in terms of future safe limits for the general population, even though exceeding those limits may present no immediate cause for concern.

CHARACTERISTICS OF AQUATIC ENVIRONMENTS THAT INFLUENCE WASTE DISPOSAL. — The role of water in the development of human culture and civilization has been almost as significant as its role in the evolution of life itself. Water not only provides the essential fluid medium in which all biochemical phenomena characteristic of life occur, but is an environmental resource so important that the volume of water in use by commercial and personal interests in the United States already approximates the total amount of water available from rainfall in the country (Anonymous 1966).

Human Use of Natural Waters. — Water is important to man primarily in two ways: a) Biological needs—we consume water as drinking water and also as an essential part of the food we eat—and b) industrial needs—here water serves mainly as coolant and diluent for carrying away excess heat and chemical wastes. As we shall see, biological and industrial needs for water conflict in many ways. The biological need for water includes farming—both agriculture and aquiculture (or mariculture). The use of water in aquiculture is obvious; in agriculture, natural rainfall is supplemented by irrigation from reservoirs or from desalinization plants, and crop production may be increased also by the use of commercial fertilizers made from seaweeds or fish meals from a distant sea.

The biological resources from aquatic ecosystems, especially from our estuaries and oceans, may be used both indirectly (fertilizers and animal feed) and directly (fish, shellfish, algae) for human food. Another biological « use » of the aquatic ecosystem is as a medium for bacterial conversion of industrial and municipal wastes either to harmless materials or to useful resources. Other uses of water include transportation (people and freight) and recreation (swimming, boating, sport fishing). Industrial contamination must be restricted so that aquatic ecosystems can maintain the capacity to support these essential functions.

Radioisotopes, along with heat and certain chemical toxins, are among the contaminants not reconverted biologically. Once diluted in the environment, radioactivity is attenuated only by physical decay. It is, however, continually cycled within the ecosystem—through plants, animals, sediments, and water. Our continued use of the aquatic environment, which no doubt will be more intensive in the future, will therefore provide many avenues for the return of discarded radioactivity to man.

Modes of Exposure to Artificial Radioactivity. — Exposure of humans to radiation from disposed waste in the aquatic environment is from external and internal sources. External exposure arises direct from contact with contaminated water, as in wading or swimming, handling fishing gear, relaxing on sandy beaches sprayed or occasionally covered with water, ... The doses received from external exposure will probably be small compared with internal doses obtained from eating radioactive seafood and drinking radioactive water. Additional internal exposure will arise from food made radioactive from fertilizers or irrigation water. How can we restrict and regulate disposal of radioactive wastes to protect humans from excessive radiation doses from the above sources? How do we transform our standards for acceptable dose level into specific limitations on radioactive contaminants released in any particular situation? The basic technique has been to restrict the concentrations of total radioactivity and of individual known radioisotopes in the environment, and more especially, in drinking water (ICRP 1960, NCRP 1959). For any given radioisotope, the concentration in drinking water which, if consumed continuously at a rate of 2.2 liters of water per day, would result in the maximum permissible dose, is called the maximum permissible concentration (MPC).

The Concept of Maximum Permissible Concentrations. — The information and assumptions needed for the calculation of a maximum permissible concentration might be illustrated best by the step-by-step development of one such MPC for a specific radioisotope. For this purpose, we have selected zinc 65, a neutron-induced radioisotope which is present in worldwide fallout and reactor effluents, and which is metabolically active in most organisms. The information and terms used for the computation of an MPC for zinc 65 in human drinking water are presented in Table 3.

Maximum permissible concentrations in drinking water for occupational exposure have been calculated (ICRP 1960) mainly by assuming that radioactive material is taken into the critical organ at the rate of P μc/day and that the biological elimination from the critical organ follows a simple exponential law. Thus, the radioactive burden of the critical organ varies with time as follows:

$$\frac{d\ (qf_2)}{dt} = P - \lambda\ (qf_2)\ \mu\text{Ci-day} \qquad (1)$$

TABLE 3

Information used for Calculation of MPC for Zinc 65 in Human Drinking Water

Term	Definition	Value for zinc 65
E	[a] Energy (Mev) absorbed by critical organ per disintegration	—
ε	[a] Effective energy $= \Sigma EF\ (RBE)n$	0.32 Mev/disintegration
F	[a] Ratio of disintegrations of daughter to disintegrations of parent	—
f_2	Fraction of q located in critical organ	1.0
f_w	Fraction of ingested radionuclide that reaches critical organ	0.1
λ	Effective decay constant = 0.693-T	0.00357
m	Mass of the critical organ (whole body)	70,000 g.
$(MPC)_w$	Maximum permissible concentration of radionuclide in drinking water	—
n	[a] Relative damage factor for radionuclides in bone	—
P	[b] Rate of uptake by critical body organ (μCi/day) $= 2200\ (MPC)_w\ (f_w)$	—
q	[c] Maximum permissible body burden $= 2.8 \times 10^{-3}\ mR/f_2\ \varepsilon$	60 μCi
R	Maximum permissible dose = 5/52 rems/week	0.098 rems-week
RBE	Relative biological effectiveness (1 for x, γ, β^-, β^+, e^- radiation)	1

T	Effective half-life $= T_rT_b/T_r + T_b$	194 days
T_b	Biological half-life	933 days
T_r	Physical radioactive half-life	245 days
t	Period of exposure = 50 years for occupational exposure	18,250 days

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[a] The effective energy term ($\Sigma EF\ (RBE)\ n$) assumes different forms for different isotopes, because of differences in decay schemes and in metabolic behavior. For different kinds of radiation, i.e., $\gamma, \beta^-, \beta^+, \alpha$, etc., E is computed differently (ICRP 1960). For γ radiation, E involves the maximum energy of the γ radiation (Mev), the fraction of the total disintegration giving rise to γ rays, the effective radius (cm) of the critical body organ, and a coefficient of absorption for the given photon energy. For zinc 65, the terms F and n are not considered because no radioactive daughter is present and zinc 65 does not principally endanger bone tissue.

[b] This calculation is based on the assumption that the average man consumes 2200 ml of water (as fluid plus foods) per day.

[c] $$2.8 \times 10^{-3} = \frac{100 \text{ erg/g rad}}{(3.7 \times 10^{4} \text{ dps}/\mu\text{Ci})\ (1.6 \times 10^{-6} \text{ ergs/Mev})\ (6.05 \times 10^{5} \text{ sec/week})}$$

If $qf_2 = 0$, then:

$$qf_2 = \frac{P\ (1-e^{-\lambda t})}{\lambda}\ \mu\text{Ci} \tag{2}$$

Substitution of appropriate values of P and λ for zinc 65 (from Table 4) and rearrangement give:

$$(\text{MPC})_w = \frac{3.16 \times 10^{-4}\ qf_2}{Tf_w\ \ (1-e^{-0.693\ t/T})}\ \mu\text{Ci/cm}^3 \tag{3}$$

Substituting values for q, f_2, T, f_w, and t (also from Table 4) gives:

$$(\text{MPC})_w = \frac{18.96 \times 10^{-3}}{19.4 - 19.4e^{-65.19}} \tag{4}$$

or

$$(\text{MPC})_w = \frac{18.96 \times 10^{-3}}{19.4} = 0.977 \times 10^{-3}$$

$$\approx\ 10^{-3}\ \mu\text{Ci/cm}^3$$

This value, $10^{-3}\ \mu\text{Ci/cm}^3$, is the concentration of zinc 65 in human drinking water that will deliver for continuous exposure a dose of 5 rems/year, the maximum dose allowed for occupational exposure (Table 2). If the maximum allowable dose is selected for some other segment of the population, the MPC must be decreased accordingly. The ICRP and NCRP have recommended MPC's for about 240 radionuclides, for occupational exposure from either air or water during a 40 hour week and during a 168 hour week. The recommended MPC for any single isotope must be diminished whenever exposure is from a mixture of radioisotopes, from air and water simultaneously, or from certain external sources of radiation. The MPC for any completely unknown mixture of radionuclides is set at $10^{-7}\ \mu\text{Ci/cm}^3$ for continuous occupational exposure.

The calculation of MPC's is entirely dependent upon biological information—data on elemental distributions and concentrations in various human organs, data on the average size of human organs and of humans themselves, data on the efficiency of accumulation of an ingested radioisotope by different organs, and data on the elimination of elements from the various organs. For many nuclides and organs, these data not only are lacking for humans, but are extremely scarce for animals. This required information has been derived from experimental results wherever possible; when facts are completely unavailable, estimates are made by comparison with chemically similar elements, or by assuming steady-state conditions for an element in a critical organ. Elemental composition and distribution for a « standard man » were first stipulated during the 1940's, but these values have since undergone many revisions and additions. The composition of the standard (or average) man was summarized by the ICRP (1960). In nearly all cases, the critical body organ is the organ that accumulates the greatest concentration of the radioisotope under consideration. The body burden (q in Table 3) is that amount of the radionuclide in the total body, which results in the maximum permissible dose to the critical organ. For many nuclides, the MPC's were computed on the bases of various critical organs. For some—e.g., zinc 65—the total body may be considered the critical organ. Because the rates and efficiencies of uptake will vary for soluble and insoluble forms of the isotope, MPC's are also presented for both physical states; often the critical organ is also different for the two forms.

It should be clear from the foregoing discussion that the protection of man from environmental radioactivity is, to say the least, a complicated problem. The discussion of MPC's, up to this point, has been limited mainly to radionuclides in drinking water. When we consider waste disposal in the aquatic environment, however, we must be concerned primarily with radionuclides in foods. Since certain elements are concentrated to very high degrees by aquatic organisms, we must reconsider MPC's in terms of human consumption of fishery products.

APPLICATION OF MPC'S TO GENERAL CONTAMINATION OF AQUATIC ENVIRONMENTS. — Evaluation of aquatic contamination by radioactivity is complicated by the diverse environmental and biological variables which affect the disposition of a radionuclide introduced into the environment. Since the greatest potential hazard to man is almost certainly from the consumption of seafood containing radioactivity, the control of waste disposal into the oceans must be such that safe concentrations in edible organisms are not exceeded. Two divergent approaches have been proposed for effecting this control: the first is merely an extension of the widely accepted MPC concept, briefly described above; and the second is based on the premise that man cannot exceed his allowable body burden of any radioisotope so long as the specific activity of that isotope in the environment is maintained below the allowable specific activity in man. We will describe both of these approaches and discuss the merits and practicality of each.

Conventional Derivation of Working Limits for Radioactivity in the Marine Environment. — Permissible concentrations of radionuclides in the marine environment are usually calculated directly from the previously recommended MPC's in drinking water for continuous occupational exposure. Since this derivation involves additional information for which supporting data may be unavailable, certain assumptions must be made. Although the limiting concentration of any radionuclide will be found in edible organisms, the approach generally followed has been to establish limits for radionuclides in sea water (NAS-NRC 1959a, 1959b; Aten 1961; Yamagata 1965; Freke 1967). A nuclear power company can readily relate such limits to the levels of radioactivity in its waste effluent. These limitations placed on environmental contamination depend very much on local conditions, and should not be misconstrued as widely applicable « standards ». Rather, they are only derived working limits (DWL) based on the already established standards for maximum permissible radiation dose.

The first step in computing a DWL for sea water is to relate the MPC for drinking water to a DWL for seafood, as follows:

$$(\mathrm{DWL})_{\mathrm{sf}} = \frac{(\mathrm{MPC})_{\mathrm{w}}\ 2200}{30\ \mathrm{I}}\ \mu\mathrm{Ci/g} \qquad (5)$$

where:

$(\mathrm{MPC})_{\mathrm{w}}$ = MPC in drinking water for continuous occupational exposure - (μCi/cm^3).

$(\mathrm{DWL})_{\mathrm{sf}}$ = Derived working limit for radioactivity in seafood (μCi/g).

I = Rate of ingestion of seafood - (g/day).

2200 = Rate of intake of water assumed for calculation of $(\mathrm{MPC})_{\mathrm{w}}$ - (cm^3/day).

30 = Factor for converting $(\mathrm{MPC})_{\mathrm{w}}$ for continuous occupational exposure to that for exposure of general population (Table 2).

Inherent in equation (5) is the assumption that the efficiency of accumulation and retention and also the final tissue distribution, i.e., f_{w}, T, and f_2 (Table 3), are the same whether the isotope is ingested in drinking water of food. Supporting data for this assumption are sorely lacking for humans. In a recent series of papers, however, researchers described experiments in which human subjects consumed whitefish (*Prosopium williamsoni*) and oysters (*Crassostrea* sp.) collected in the Columbia River downstream from the reactor effluent. Accumulation of zinc 65 from these sources did not follow exactly the pattern predicted by application of the ICRP « standard man » values of 10 percent fractional absorption (f_w) and 194 days effective half-life (T). An experiment with only one subject eating whitefish gave $f_w = 32$ percent and $T = 162$ days (Foster and Honstead 1967). This fractional absorption of zinc 65 from whitefish was later confirmed in a 7-subject experiment by an average value of $F_w = 35$ percent (Honstead and Brady 1967). Accumulation of zinc 65 from oysters (again only one subject) gave $f_w = 13.5$ percent and $T = 100$ days (Honstead and Hildebrandt 1967). Although the sources of these differences are unknown, it is clear that the ICRP assumptions on radioisotope accumulation and retention are not necessarily exact for accumulation from various foods. Zinc 65 is absorbed more readily from oysters and fish than the ICRP assumed for uptake from drinking water. If this discrepancy is a general phenomenon, then DWL values for foodstuffs calculated by equation (5) will need to be decreased accordingly.

One possible explanation for the differences in efficiency of assimilation is that transport of zinc across the mucosa is facilitated by the presence of protein in the gut. The circumstantial evidence for this hypothesis is presented in Table 4.

TABLE 4

Protein Content of Food and Uptake of Zinc 65 from Different Sources

Source	Efficiency of Assimilation f_w	Percentage Protein Content P_c
Drinking water	.10[a]	—
Oysters	.135[b]	6.0[c]
Fish	.35[d]	17.9[c]

[a] ICRP (1960).
[b] Honstead and Hildebrandt (1967).
[c] Diem (1962).
[d] Whitefish - Honstead and Brady (1967).

A more probable explanation, which is completely unsupported at present, is that both assimilation efficiency and retention of an element depend on the total amount of that element in the diet.

The $(DWL)_{sf}$ calculated by means of equation (5) refers to the radioactivity in the food when it is consumed, not when it was caught. Applying this $(DWL)_{sf}$ to organisms while still in the environment would result in a safety factor for humans because physical decay of the radioactivity occurs during the interim between capture and consumption of the seafood. This factor is of little consequence for long-lived nuclides such as cesium 137 and strontium 90, but could permit elimination by decay of short-lived isotopes such as iodine 131. The $(DWL)_{sf}$ obviously refers also to the average concentration of radioactivity in any species of seafood eaten. Since many species of fish migrate during their life-spans, the variation of radioactivity among individuals may be high. Individual fish containing high levels of radioactivity will be diluted (in the natural population, and during commercial processing and marketing) by fish which are from other geographical areas and contain less radioactivity. « Market dilution » can be accounted for by permitting organisms in the immediate area of waste disposal to contain more radioactivity than is allowable for the average seafood consumed. A factor of 10 for this dilution has been suggested (Dunster 1958).

The rate of ingestion of seafood—I in equation (5)—should approach the maximum amount eaten daily by any individual, but must obviously be an approximate value. A reasonable approach would be to estimate the maximum intake for one year, then pro-rate the intake on a daily basis. People in different geographical locations and in different socio-economic or ethnic situations consume vastly different amounts and kinds of seafood. Various estimates of intake appear in the literature (Aten 1961; Yamagata 1965; NAS-NRC 1959a, 1959b; Weaver 1967). Values generally range from 110 to 250 g seafood consumed per day, and are based on the partial or complete fulfillment of the average dietary protein requirement by seafood. Freke (1967) did not specify an average intake, but defined I in terms of an average daily protein requirement of 1 g protein per kg body weight;

$$I = \frac{100\ (70)}{P_c} \tag{6}$$

where:

P_c = Percent protein content of seafood in question.
70 = Body weight in kg of standard man.

If we take the approach used for MPC's in drinking water, we assume that the entire protein consumption of the population is from seafoods and that the seafood constitutes the only source of radioactivity. The second assumption is already inherent in the calculation. To match the average protein consumption in the United States, a man would have to eat approximately 1.8 kg of fish per week (NAS-NRC 1959a), or $I = 260$ g/day. The $(DWL)_{sf}$ based on this value for I would be $\frac{2200}{260}$, or about 8.5 times the $(MPC)_w$ for the general population; would have to be reduced to allow for other internal sources of radioactivity, including those from drinking water and other foods.

From the viewpoint of public health protection, it would probably be most practical to establish maximum levels of radioactivity for various types of foodstuffs, including seafood. This approach, however, is not practical for the control of waste disposal. Effective limits for controlling the rate of discharge of radioactivity into marine environments necessarily must be based on maximum levels for seafood, but must be expressed in terms of DWL's for the radioactive effluent (Aten 1961) or as maximum permissible rates of release, in curies per day (Freke 1967).

Derived working limits for sea water are obtained directly from $(\mathrm{DWL})_{\mathrm{sf}}$ by dividing the ratio of the elemental concentration in the seafood to that in the sea water (concentration factor).

$$(\mathrm{DWL})_{\mathrm{sw}} = \frac{(\mathrm{DWL})_{\mathrm{sf}}}{\mathrm{C_f}} \qquad (7)$$

It is evident that the value of $(\mathrm{DWL})_{\mathrm{sw}}$ for any particular radioisotope depends entirely upon which organism is considered in the calculation. Widely different values for $\mathrm{C_f}$ have been reported for the same element or isotope among different groups of edible marine organisms. Since metabolic uptake and physical adsorption are both affected by physical conditions such as temperature, pH, and salinity, concentration factors for a given isotope in any single species must also be subject to wide variation. Concentration factors for different elements in aquatic organisms have only recently been compiled from the literature by Polikarpov (1966). Varying patterns of consumption of any given seafood species also affect $(\mathrm{DWL})_{\mathrm{sf}}$, so that the $(\mathrm{DWL})_{\mathrm{sw}}$ is a particularly vulnerable criterion. Freke (1967), in his derivation of $(\mathrm{DWL})_{\mathrm{sw}}$, selected a single reasonable (or acceptable) value of $\mathrm{C_f}$ from the literature for each of a long series of radionuclides in four different groups of seafood organisms: fish, crustacea, molluscs, and seaweed. A similar, though less restrictive, approach presented by NAS-NRC (1959a) discriminated only between vertebrates and invertebrates. The group of organisms exhibiting the greatest $\mathrm{C_f}$ is considered limiting, and the $(\mathrm{DWL})_{\mathrm{sw}}$ was computed on that basis.

Let us now complete our example. Zinc 65 generally is concentrated by oysters (*Crassostrea virginica* Gmelin) about 100,000 times the sea water concentrations of the isotope. For our purposes, we will consider this the limiting factor for zinc 65 in sea water. Thus, we have, from equations (5) and (7):

$$(\mathrm{DWL})_{\mathrm{sw}} = \frac{2200\ (\mathrm{MPC})_{\mathrm{w}}}{30 \times \mathrm{I} \times \mathrm{C_f}}\ \mu\mathrm{Ci/cm^3} \qquad (8)$$

where:

$(\mathrm{MPC})_{\mathrm{w}} = 10^{-3}\ \mu\mathrm{Ci/cm^3}$
$\mathrm{I} = 260\ \mathrm{g/day}$
$\mathrm{C_f} = 10^5$

and:

$$(\mathrm{DWL})_{\mathrm{sw}} = \frac{2200 \times 10^{-3}}{30 \times 260 \times 10^5} = 2.8 \times 10^{-9}\ \mu\mathrm{Ci/cm^3}$$

If equation (6) is used to calculate I (using $P_c = 6.0$, from Table 4), then $I = 1170$ g/day and $(DWL)_{sw} = 1.26 \times 10^{-10}$ μCi/cm^3. As is usually the case in estimating concentration factors, grams and milliliters are considered equivalent in equation (8). The foregoing estimation of $(DWL)_{sw}$ is fraught with uncertainty. As discussed previously, the factors I and C_f are subject to wide variability, and uptake of an isotope from seafood is not necessarily equatable to uptake from drinking water. Perhaps the greatest uncertainty, however, arises from the arbitrary selection of a single species (necessarily one for which information is available) as the basis of the entire calculation. No single species is consumed at a uniform rate by the entire population. The use of an « average » value of C_f for a large group of similar organisms, e.g., molluscs, is also unacceptable, because certain species that constitute a significant part of the diets in certain localities may exhibit much higher concentration factors. Many of these drawbacks are eliminated from consideration in the application of the specific activity approach.

Derivation by Specific Activities of DWL's for Marine Environment. — The use of specific activity for establishing permissible levels of environmental radioactivity was first recommended for radioactive waste disposal into U. S. Pacific coastal waters (NAS-NRC 1962). Specific activity of any radioisotope is defined as the ratio of the amount of the radioactive isotope to the total amount of the element present (μCi/g, or equivalent). The application of this approach is based mainly on two assumptions: 1) that a radioisotope introduced into the environment readily equilibrates with the stable isotope (s) of the same element such that biological concentrating mechanisms will be unable to discriminate between the radioactive and stable forms, and 2) that the quantity of each stable element in each body organ is « fixed » and does not fluctuate with the intake of that element. Thus the distribution of radionuclides will correspond to the distribution of stable elements in the environment. The maximum permissible specific activity (MPSA) for any radioisotope with a critical organ other than the gastrointestinal tract is readily available from data on the standard man (ICRP 1959):

$$(MPSA) = \frac{q}{m \times C} \tag{9}$$

where:

(MPSA) = Maximum permissible specific activity (μCi/g).

q = Maximum permissible burden of radioisotope in critical organ (μCi).

m = Mass of the critical organ (g).

C = Concentration of stable element in critical organ (g/g).

The (MPSA) is then converted to $(DWL)_{sw}$ (or, if desired, $(DWL)_{sf}$) simply by multiplying by the concentration of stable element in sea water (or in the seafood):

$$(DWL)_{sw} = K \times (MPSA) \qquad (10)$$

where K = grams of stable element per cm^3 sea water.
The $(DWL)_{sw}$ so derived is independent of concentration factors and of rate of consumption of seafoods. If the MPC is set for sea water instead of for marketed seafood, then physical decay of the radioisotope will introduce a safety factor. Radioactivity accumulated by primary producers and then passed up a food chain to man will undergo physical decay during its residence in each trophic level. This process will be partially offset by continuous bioaccumulation from the water surrounding the organism, but for most elements the biological turnover is slow enough for physical decay to reduce significantly the specific activity of a radioisotope before the organism is consumed by organisms in the next higher trophic level. The extent of attenuation obviously depends on the physical half-life of the radioisotope and the residence time of the isotope in each trophic level.

The specific activity approach, as calculated in equations (9) and (10), should be applicable for any situation where the gastrointestinal tract is not a critical organ. For those radioisotopes which are not assimilated efficiently, the primary concern must be for the gastro-intestinal tract, and the $(DWL)_{sw}$ must be derived from the allowable radioactivity estimated for seafood organisms, as by equations (5) and (7). The shortcomings of this technique were discussed previously. The MPSA for an isotope with the gastro-intestinal tract as a critical organ could be calculated from the $(DWL)_{sw}$ and the elemental concentration in sea water (equation (10)). The specific activity approach might also be invalid in individuals that had consumed food and water containing the MPSA of a radioisotope for a very long time. In such a case, the body burden of the isotope would approach the maximum permissible body burden (but never reach it because of physical decay of the isotope during its metabolism) such that consumption of a meal containing high radioactivity, but still no more than the MPSA, would result in more than the maximum allowable burden for either the gastro-intestinal tract or the total body. This potentiality is of little immediate consequence, because environmental radioactivity certainly does not approach the MPSA's except (possibly) in extremely localized areas.

Certain examples of bioaccumulation have led investigators to question the premise that radioisotopes behave in the natural environment just as does the stable isotope of the element. For example, Schelske et al. (1966) postulated that bay scallops (*Aequipecten irradians* Lamarck) accumulated manganese 54 from particulate fallout in sea water because the specific activities of scallop tissues were higher than the specific activity of the water.

The results of calculating $(DWL)_{sw}$ for several isotopes by the specific activity and the conventional approach are compared in Table 5 (Isaacs 1964).

TABLE 5

Comparison of $(DWL)_{sw}$ Values Derived by Conventional and Specific Activity Approaches[a]

(1) Isotope	(2) PSC[b] conventional approach (μCi/ml)	(3) MPCC[c] specific activity approach (μCi/g)	(4) (2)/(3)
Cobalt 60	5×10^{-9}	5.0×10^{-9}	1.0
Iron 59	3×10^{-9}	3.0×10^{-9}	1.0
Copper 64	6×10^{-9}	6.0×10^{-9}	1.0
Zinc 65	2×10^{-8}	1.2×10^{-8}	1.67
Cesium 137	4×10^{-6}	1.5×10^{-4}	0.0267
Strontium 90	5×10^{-8}	3.4×10^{-5}	0.00147
Iodine 131	2×10^{-9}	1.6×10^{-6}	0.00125
Phosphorus 32	1×10^{-9}	2.8×10^{-9}	0.357
Sulphur 35	1.2×10^{-5}	8.4×10^{-3}	0.00143
Calcium 45	4.5×10^{-6}	1.2×10^{-4}	0.0375

[a] Modified from Isaacs (1964).

[b] Permissible sea water concentrations as calculated in NAS-NRC (1959 a) but revised according to NRCP (1959) values for $(MPC)_w$, and according to the more recent biological concentration factors and the appropriate reduction factors for dose to the general population as recommended by NAS-NRC (1962).

Maximum permissible sea water concentrations recommended by NAS-NRC (1962). All values except those for cobalt 60, iron 59, and copper 64 were calculated by equations (9) and (10), but were then increased by decay factors appropriate for the physical and biological half-lives of each isotope.

Table 5 shows that the specific activity approach usually gives less stringent standards for radioactive waste in sea water. Since the first three nuclides in Table 5—cobalt 60, iron 59, and copper 64—have the gastro-intestinal tract as the critical organ, the derivations necessarily are identical, i.e., by equations (5) and (7). For other isotopes the specific activity approach permits up to almost 1000 times as much environmental radioactivity in sea water. It should be emphasized that the MPCC values (Table 5, column 3) were intended to represent the actual *limits of safety* for radioactivity in sea water, whereas the conventional approach (Table 5, column 2) includes many poorly defined safety factors. The specific activity approach has the following drawbacks: 1) it is not valid when considering radiation dose to the gastro-intestinal tract; 2) as a human approaches his maximum permissible body burden of radioactivity, the *total* activity of the contents of his gastro-intestinal tract becomes significant, regardless of what the *specific* activity is; and 3) radionuclides introduced into the environment may be more (or less) readily available for bioaccumulation than the corresponding stable element, i.e., the entire basis for the approach may at times be invalid.

The specific activity approach has special merit for those radioisotopes which, because of long physical half-life or of continuous introduction into the environment, are chronic contaminants. Such radioisotopes will have had ample time to equilibrate with the stable isotopes already present in the environment, so that after the initial period of introduction, most of the radioisotope will be distributed in the same way as a stable carrier. Such is probably the case with cesium 137 and strontium 90 from fallout in the biosphere, although neither isotope has yet equilibrated in the deeper parts of the ocean (Broecker, Bonebakker, and Rocco 1966). In any acute contamination, however, the radioisotopes may be introduced in a physical or chemical form different from that of the stable isotopes in the environment, and bioaccumulation of the radioactivity might be independent of the distribution of the stable element. At present, nearly all radioactivity introduced into the environment is comparable to acute contamination, because significant concentrations of most radioisotopes are not yet widespread, but are localized in the immediate areas of contamination. As radioactive contamination becomes widespread, i.e., as portions of the environment approach their « maximum permissible burdens » of radioactivity, the specific activity approach will become increasingly applicable. In the meantime, isolated instances of « acute » radioactive contamination might be controlled more effectively on the basis of the nature of the contaminating effluent and of the immediate environmental circumstances than on the basis of the distribution of stable elements in the receiving environment. The conventional approach necessarily involves many conservative approximations but nevertheless is based on sound principles of bioaccumulation, and will adequately protect the population from excessive radiation.

The techniques we apply to the problem of radioactive contamination of our environment must undergo continuous revision as new information develops.

Limits on the quantities of water-borne radioactive materials that can be released to the environment are now based on the expectancy that the receiving water will be used as a source of drinking water or that people will consume large quantities of fish, shellfish, or other aquatic or marine foodstuffs produced in the vicinity of the plant discharge. The calculations that lead to the specification of release rates (or maximum concentrations of radionuclides in the effluent) are based on conservative estimates of the behavior of the radionuclides in the receiving water, the reconcentration of certain radionuclides by aquatic and marine food organisms, the rates of consumption of edible parts of the food organisms, and the accumulation and retention of the nuclides in man. Many of the estimates now used are tentative and are probably overly conservative because of a paucity of definitive data.

Additional radioecological research is underway in many laboratories through the world to improve the estimates that are now being used, to provide greater assurance of the safety of the limits as now calculated, and to acquire the knowledge needed to cope with unplanned radioactive contamination. Further research is especially needed on the following:
1) the fate of radioactive materials discharged into natural waters, 2) the reconcentration of radionuclides by important aquatic organisms, 3) the efficiency of transfer of radionuclides through food webs, 4) the flux of acute releases of radioactive wastes through aquatic communities, and 5) the effects of chronic exposure to low levels of radioactive materials on aquatic organisms and populations. Continued research in these areas will ensure that we are neither too permissive nor excessively restrictive in our regulation of radioactive waste disposal into aquatic environments.

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D. A. Wolfe and T. R. Rice

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DISTRIBUTION AND ABUNDANCE OF THE JAPANESE SNAIL, *VIVIPARUS JAPONICUS*, AND ASSOCIATED MACROBENTHOS IN SANDUSKY BAY, OHIO[1, 2]

DAVID R. WOLFERT AND JARL K. HILTUNEN

United States Department of the Interior, Bureau of Commercial Fisheries, Sandusky, Ohio, and *Ann Arbor, Michigan*

ABSTRACT

A survey of the macrobenthos of Sandusky Bay, Lake Erie, in June, 1963, provided information on the abundance and distribution of the introduced Japanese snail, *Viviparus japonicus*, which has become a nuisance to commercial seine fishermen. The abundance and distribution varied considerably within the bay; at the time of the survey, most snails were found near the north-central shore. Environmental characteristics were nearly uniform and had no apparent effect on the distribution; concentrations in different areas at different times appeared to result from water movements induced by winds. The time of the study coincided with a period of reproduction; young-of-the-year snails were most abundant in areas where adults were most common. The frequency distributions of shell height and diameter suggested the presence of two age groups of adults in the population. Considerable natural mortality was seen, both at the time of the study and in other seasons. Only three other gastropods were observed in the bay; the most abundant was another viviparid, *Campeloma decisum*. Other mollusks present were four species of Sphaeriidae and 18 species of Unionidae. A summary of invertebrates found, other than the mollusks, is also presented.

INTRODUCTION

Great numbers of the Japanese snail, *Viviparus japonicus*, are sometimes caught by commercial seine fishermen in Sandusky Bay, Lake Erie. This species has become a nuisance in the commercial fishery, primarily during the spring fishing season. Local fishermen have reported that they sometimes catch two tons in a seine haul. Although no records are available concerning the time of introduction of the Japanese snail into the bay, fishermen in the area recall that one bushel of these animals was brought from Maryland by Clinton Reiley in the 1940's and stocked as a possible food for channel catfish, *Ictalurus punctatus*, an important species of commercial fish in western Lake Erie. The nuisance caused by the Japanese snail prompted this survey to determine its distribution and abundance in the bay and to evaluate the associated macrobenthos.

Published records of the distribution of the Japanese snail in the United States are few. Hannibal (1911) and Johnson (1923) recorded it from California and Massachusetts, respectively. It has become widespread, particularly in the north-central and northeastern states (Clench, 1962). We have seen specimens from Green Bay, Lake Michigan, and from the extreme western shore of Lake Erie, as well as from Sandusky Bay.

Two other species of *Viviparus* listed from North America (Walker, 1918), *V. contectoides* and *V. malleatus*, are found in the Great Lakes region. The latter has been collected in bottom trawls near the Bass Islands in western Lake Erie.

PHYSICAL CHARACTERISTICS OF SANDUSKY BAY

Sandusky Bay, located on the south shore of western Lake Erie, is 24.0 km long and 6.5 km wide. Two causeways at Bay View, Ohio, divide it into the Upper Bay and the Lower Bay (fig. 1a). Subsequent to this study, another causeway was constructed about 0.5 km west of the west causeway shown in figure 1a.

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The margin of the Upper Bay is predominantly marshland; that of the Lower Bay is elevated and its south shore is occupied largely by industry or dwellings. The marshland is occasionally flooded by lake water forced into the bay by strong northeasterly winds.

The maximum natural depth of the bay is less than 4.0 m. The shipping channel from Cedar Point to the city of Sandusky, however, is dredged to a depth of 6.1–7.6 m. Bottom composition is mostly mud, with a few small scattered patches of a mixture of gravel, sand, and mollusk shells. Rooted bottom vegetation is sparse and consists mainly of small beds of sago pondweed, *Potamageton pectinatus*. The combination of shallow water, mud buttom, scanty bottom vegetation, and frequently shifting winds causes the bay waters to be perpetually turbid. Secchi disk measurements are usually less than 0.3 m. Surface water temperatures have been known to reach 30° C in the summer. Bottom water temperatures ranged from 16° to 24° C during our investigation, June 4–21, 1963.

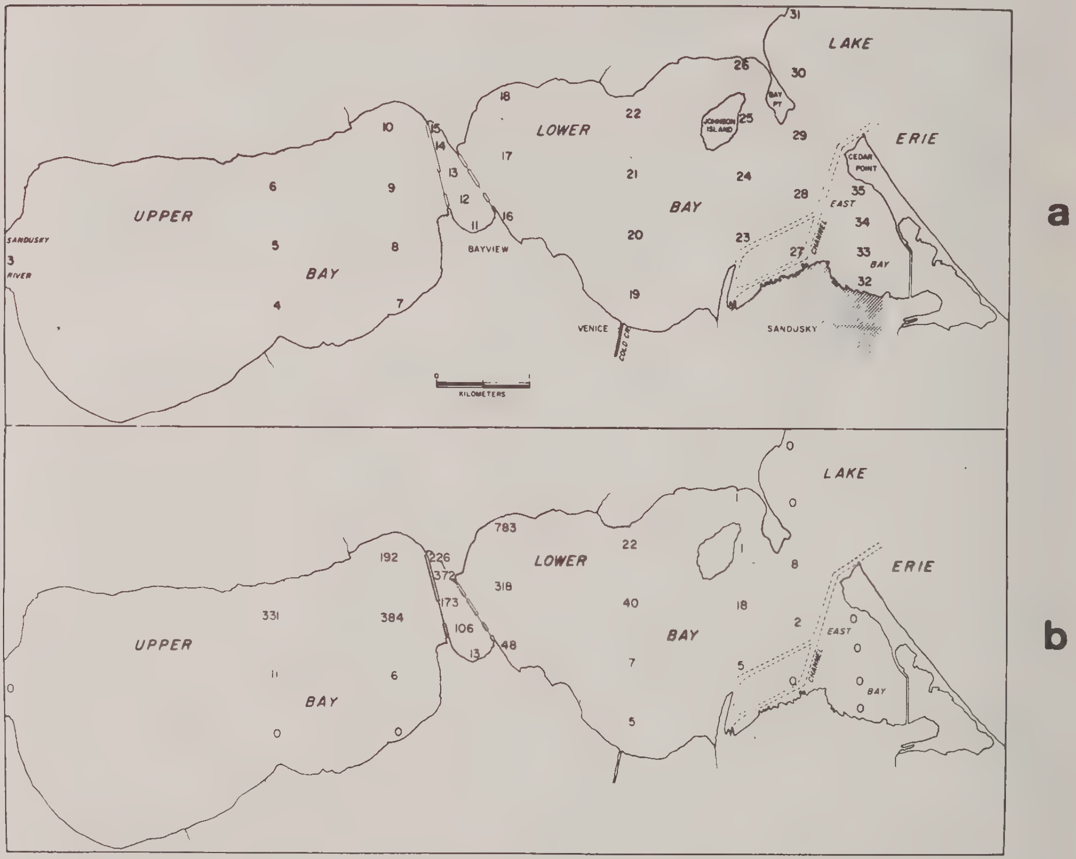
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FIGURE 1. Map of Sandusky Bay showing location of stations where samples were collected (a), and numbers of *Viviparus japonicus* collected by trawl at each station (b). Stations 1 and 2, in the Sandusky River, are not shown.

MATERIALS AND METHODS

Bottom samples were taken at 35 stations about ¼ and ½ mile (0.4 km and 0.8 km) apart, usually on north-south lines across Sandusky Bay (fig. 1a). Data collected at each station were bottom water temperature, depth, sediment type, and abundance of mollusks and other macrobenthos. The temperature of bottom water was measured with a resistance thermometer.

Large mollusks were sampled with a 16-foot semiballoon otter trawl with ½-inch-mesh cod end (stretch measure). A chain was attached to the foot rope of the trawl to help ensure the collection of specimens that were partially buried in the sediment. The trawl was towed by a 16-foot outboard motorboat at 2–3 mph (1.7–2.6 knots) for 5 minutes. One tow was made at each station. Each tow covered about 0.1 hectare of bottom. An otter trawl was also used with "moderate" success by Stansbery (1961) to collect naiad mussels near South Bass Island, Lake Erie.

Bottom samples for other macrobenthos were taken initially with a Petersen dredge (stations 32–35), but it was too awkward and heavy for use from a small boat; a 6- by 6-inch Ekman dredge was used at the remaining stations. Three dredge samples were taken at each station. Samples were washed through a U. S. standard No. 30 wire screen and the residue was preserved in 5-percent formalin for later examination.

All mussels were first immersed in a solution of sodium nembutal, a relaxing method described by van der Schalie (1953), then fixed in 10-percent formalin. Ultimately, some were transferred to 95-percent ethanol and others were transferred to a saturated aqueous solution of propylene phenoxytol. Both preservatives were effective.

Gastropods resisted relaxation in nembutal and consequently could not be fixed properly. Crystalline menthol dissolved in warm water and methanesulfonate (M.S. 222) were tried as relaxants, but were ineffective. Personnel of the U. S. Bureau of Commercial Fisheries sea lamprey research program suggested 3 compounds which they had found to have a relaxing effect on some mollusks. These chemicals were α-styrylpyridine, 3-trifluormethyl-4-nitrophenol (TFM), and 3,4,6-trichloro-2-nitrophenol. Bioassay tests of these 3 compounds at 10, 20, 30, 40, 50, 60, and 70 ppm were made at ambient room temperatures (20°–25° C). Little or no relaxation was evident after 24 hours in the α-styrylpyridine and TFM solutions. However, all specimens in the 40- and 50-ppm solutions of 3,4,6-trichloro-2-nitrophenol (Dow Chemical Company, Midland, Michigan) were relaxed. Upon immersion in 10-percent formalin, the snails did not withdraw and later examination revealed that fixation was satisfactory.

THE JAPANESE SNAIL

The Japanese snail is viviparous and the largest operculate snail in the Great Lakes. At birth the shell of the young is approximately 5.5 mm in height and 4.5 mm in diameter. It is shaped like a toy top, pallid in color, and has rows of epidermal bristles on the whorls that disappear as it grows. In the adult, the shell is a deep brown and the whorls are inflated, or more rounded, than in the young. The only external feature that we found to distinguish sex was the modified (blunter, shorter, and thicker) right tentacle of the adult male (fig. 2). This organ is similarly modified in both the juvenile and adult *V. contectoides* (Van Cleave and Lederer, 1932), but in the juvenile Japanese snail we found no such dissimilarity.

The 3,787 specimens collected from Sandusky Bay included two size groups: juveniles that were less than 10 mm high and adults that were more than 30 mm high. Three adults and 9 juveniles were taken in dredge samples; all others were caught with the trawl.

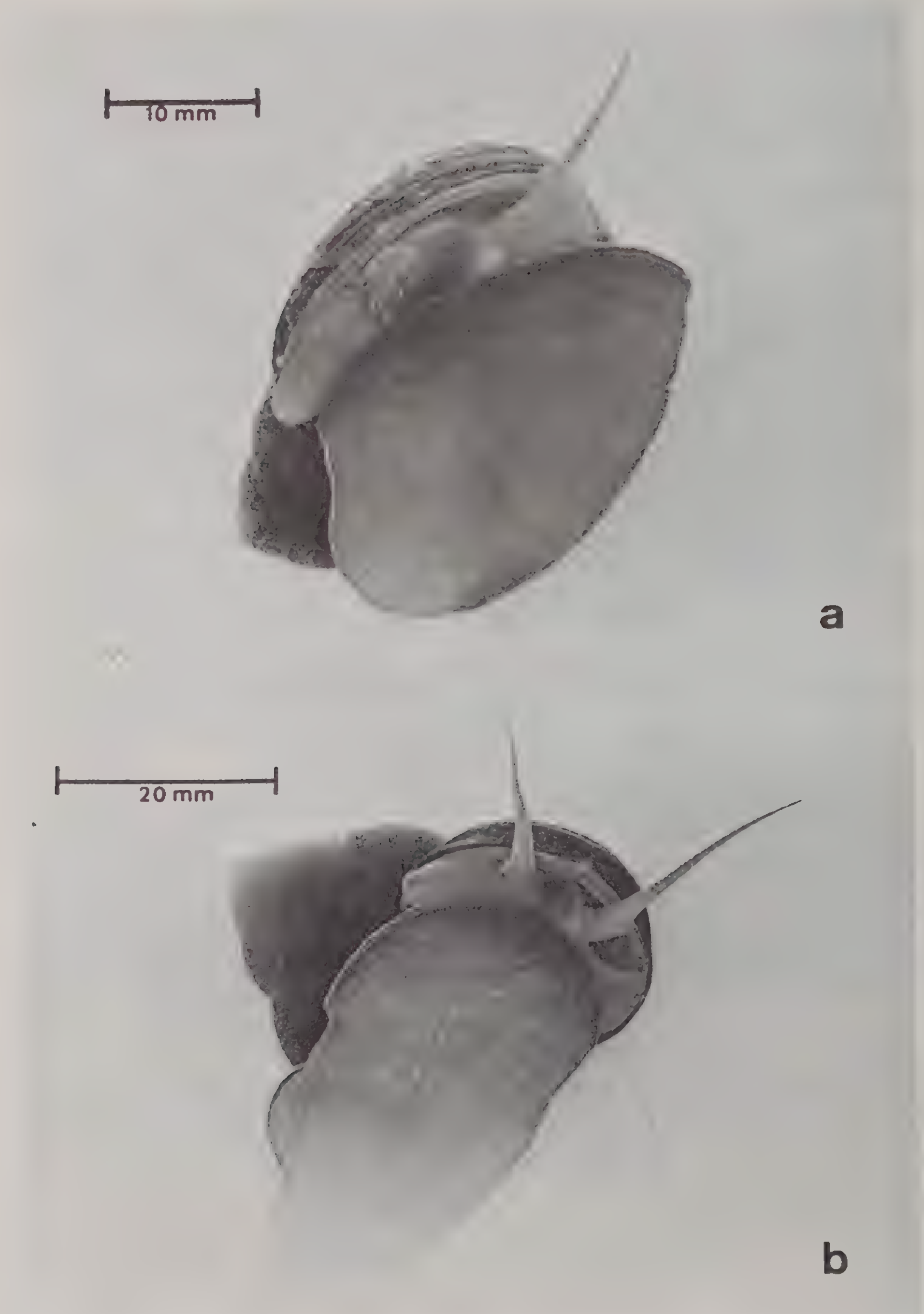

FIGURE 2. *Viviparus japonicus* from Sandusky Bay, Ohio: adult male (a), and adult female (b).

Distribution and Abundance

The abundance of adult Japanese snails varied considerably from station to station during our survey. The greatest numbers were taken at stations near the north shore of the central portion of Sandusky Bay (fig. 1b). The largest catch was 783 snails taken in a single trawl haul at station 18. Few adults were found along the southern shore; none were captured in similar hauls made in the southeast corner of the Lower Bay, although we have frequently seen them in the marshes along the southeast extremity of the Lower Bay in water a few centimeters deep. No Japanese snails were taken at the two stations in Lake Erie just outside the mouth of the Lower Bay. None were taken at the mouth of the Sandusky River (station 3); two were captured at station 2 near the mouth, but none were taken at station 1, about 0.8 km upstream.

The distribution of Japanese snails in Sandusky Bay is variable and seems to be influenced by the wind. The heavy concentrations along the northern shore probably resulted from the southerly winds that occurred during the period of investigation. In the time since our survey, we have often observed large numbers of snails taken by seine fishermen along the south shore after a period of strong northerly winds. Conversely, after strong southerly winds, the catch of snails along the north shore increases. This shift in the distribution is probably a direct result of water movements caused by the prevailing winds. Depth, bottom type and character, turbidity, and water temperature seemingly have little effect on the distribution of the snail, for these characteristics are nearly uniform throughout the bay.

Juvenile (young-of-the-year) snails were taken at 15 of the 35 stations. The number taken by trawl, however, was probably not an accurate measure of the population density of juveniles, because the mesh size of the trawl was large enough to permit the escape of many.

Young were most abundant in areas where adults were most common, presumably because the time of the collections coincided with a period of reproduction; live females held in the laboratory at this time produced many young. The largest number of young snails taken in a single tow was 239, in the west-central part of Lower Bay (station 17). In north-central Upper Bay (station 6), where 146 live young were taken, about 150 dead snails and empty shells of young were also found. Very few dead snails or empty shells of young were observed at other stations.

Age Composition

Frequency distributions of measurements of greatest shell height and diameter of 294 adult Japanese snails were made in an attempt to distinguish age groups (fig. 3). Van Cleave and Lederer (1932) have shown that the males of *V. contectoides* are smaller than the females. Although we noted among the larger Japanese snails that the males tended to be slightly smaller than the females, we did not measure the sexes separately to determine the degree of sexual dimorphism. Greatest shell diameters for the combined males and females ranged from 22 to 46 mm, and greatest heights from 30 to 65 mm; both measurements showed a bimodal distribution, suggesting that two age groups of adults were present. We believe that each mode is composed of the males and females of a single age group, and that the smaller individuals of each mode are predominantly males and the larger ones females.

Natural Mortality

During a preliminary survey of the area in March, 1963, many decomposing Japanese snails were seen floating in the bay. This mortality probably resulted from winter kill, old age, or both. Considerable mortality was also noticed in the marshes bordering the bay during the summer, when the marshland was drying up and many snails were stranded on hard, sun-baked mud and clay.

ASSOCIATED MACROBENTHOS

Although the Japanese snail was our primary concern, gross observations of associated invertebrates taken at each station were also made. The most common organisms were gastropods (other than the Japanese snail) and pelecypods (table 1). A synopsis of macrobenthos other than mollusks is given in table 2.

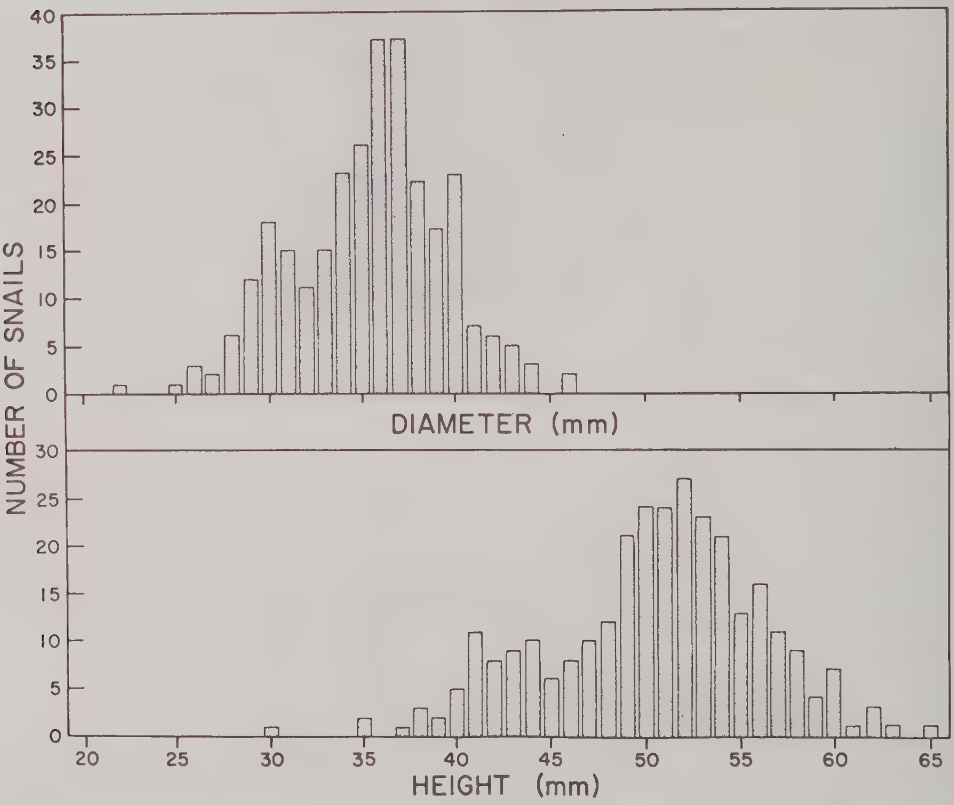

FIGURE 3. Frequency distributions of greatest shell height and greatest shell diameter of 294 adult *Viviparus japonicus* from Sandusky Bay.

Gastropoda

The second-most-abundant snail in the bay was another viviparid, *Campeloma decisum*. It was distributed throughout the entire bay, but was most abundant near the mouth of Sandusky Bay, where nearly 90 percent of the 72 specimens were taken. The distribution of *Pleurocera acuta* was scattered, although nearly 45 percent of the specimens were collected from the protected area between the two causeways (stations 11–15). One *Bulimus tentaculatus* was obtained (station 23); because no individuals of this small species were taken by dredge, we concluded that the species was sparsely distributed.

TABLE 1

*Number of mollusks taken in trawl hauls and dredge samples from Sandusky Bay, Lake Erie, in June 1963, listed in order of abundance**

species	trawl hauls	dredge samples
Gastropoda		
Viviparus japonicus (van Martens)		
Adult	2,972	3
Juvenile	803	9
Campeloma decisum (Say)	57	15
Pleurocera acuta Rafinesque	18	0
Bulimus tentaculatus (Linnaeus)	1	0
Pelecypoda		
Sphaeriidae		
Sphaerium transversum (Say)	147	73
Pisidium henslowanum (Sheppard)	0	9
Pisidium compressum Prime	0	1
Pisidium casertanum (Poli)	0	1
Unionidae		
Lampsilis siliquoidea (Barnes)	63	0
Truncilla donaciformis (Lea)	62	0
Carunculina parva (Barnes)	16	1
Proptera alata (Say)	14	0
Obliquaria reflexa Rafinesque	11	0
Anodonta grandis Say	10	0
Quadrula pustulosa Lea	7	1
Truncilla truncata Rafinesque	7	0
Quadrula quadrula (Rafinesque)	5	0
Amblema costata Rafinesque	5	0
Leptodea fragilis Rafinesque	4	0
Ligumia recta latissima (Rafinesque)	3	0
Fusconaia flava (Rafinesque)	3	0
Ligumia nasuta (Say)	2	0
Pleurobema cordatum coccineum (Conrad)	1	0
Lampsilis ventricosa (Barnes)	1	0
Elliptio dilatatus (Rafinesque)	1	0
Anodonta imbecillis Say	1	0

*The classification of the snails follows Goodrich (1932) and Berry (1943); the Sphaeriidae follow Herrington (1962); and, the Unionidae are classified according to Heard and Burch (1966).

Pelecypoda

The family Sphaeriidae was represented by species of *Pisidium* and *Sphaerium*, which are common in Lake Erie. *S. transversum*, a species very abundant at the mouth of the Detroit River (Carr and Hiltunen, 1965), was the most abundant fingernail clam in Sandusky Bay. Although it is not large in size, it was so abundant that many, including nepionics, were captured even in the trawl. The greatest concentration was in the Lower Bay. Sixty-six percent of all *S. transversum* taken by both trawl and dredge were from stations 17 and 18, where adult Japanese snails were also most abundant. Dredge samples from these stations yielded 1,048 *S. transversum* per m^2. At station 6, all individuals (15) of this species caught were dead; because no decomposition was apparent, the mortality must have been recent. This was the station from which the many empty shells of juvenile Japanese snails, discussed previously, were obtained.

A total of 216 Unionidae were taken with the trawl. Almost 50 percent were caught at stations 13, 17, and 29. *Lampsilis siliquoidea* and *Truncilla donaciformis* made up nearly 58 percent of all unionids taken.

Langlois (1954) listed 33 unionid species that have been reported from western

Lake Erie. Carr and Hiltunen (1965) discovered one additional species (*Leptodea laevissima*). In the present study, 18 of these species were found in Sandusky Bay.

TABLE 2
Summary of invertebrates other than mollusks in Ekman dredge samples from Sandusky Bay, Lake Erie, June 4–21, 1963

Taxonomic group	Remarks*
Hydra spp.	Present at stations 30 and 35.
Nemata	Present in nearly all samples.
Bryozoa	Found on *Viviparus japonicus* shells at few stations.
Hirudinea	One collected at each of stations 17 and 27.
Oligochaeta	Group well represented at all stations. *Branchiura sowerbii* Beddard most common; present at all but 7 stations. Greatest number (24) found at station 31.
Polychaeta	Twenty-three *Manayunkia speciosa* Leidy found only at station 35.
Cladocera and Copepoda	Present at all stations. Most numerous at stations 30 and 31. *Leptodora kindtii* (Focke) frequently present.
Amphipoda	*Gammarus* sp. present at 4 scattered stations; most (6) were at station 23.
Isopoda	One *Asellus militaris* Hay taken at each of stations 17, 24, and 30 and 4 at station 23.
Diptera	Heleidae were present at 6 stations. Tendipedidae were present at all but 3 stations. *Coelotanypus concinnus* (Coquillett) and species of *Tendipes*, *Procladius*, and *Pelopia* predominated. One specimen of *Chaoborus* sp. was found at station 3.
Ephemeroptera	*Hexagenia* sp. was found at 10 stations, most of which are in the Lower Bay. Number of individuals present at each station ranged from 1 to 3. Three specimens of Caenidae were present at station 23. One unidentified specimen taken at station 16.
Trichoptera	One specimen of *Oecetis* sp. was collected at station 26.
Hydracarina	Present at 6 scattered stations.

*See figure 1 for location of stations.

ACKNOWLEDGMENTS

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Most of the mollusks collected have been deposited in the Museum of Zoology of The University of Michigan.

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Proceedings of the National Shellfisheries Association
Volume 58 — June 1968

ABSTRACT

SURF CLAM RESEARCH, 1966

Robert M. Yancey

U. S. Bureau of Commercial Fisheries
Biological Laboratory
Oxford, Maryland

In our continuing study of surf clams (*Spisula solidissima*), four major research areas were investigated in 1966: fishery statistics, population densities and distribution, growth rates, and reproduction.

Port sampling, interviews with boat captains, and day trips aboard the fishing vessels provided information on fishing areas, catch, effort, clam lengths, and amount of small clams discarded at sea. The major fishing areas are off Point Pleasant and Cape May, New Jersey, in depths of 24 to 110 feet. Point Pleasant and Cape May-Wildwood are the principal ports. Average daily catch per boat was 328 bushels of clams and average catch per hour was 38 bushels. Boats fished an average of 9 hours a day. Average length of clams landed was 151 mm at Point Pleasant and 130 mm at Cape May-Wildwood. The amount of clams discarded at sea was negligible.

Two research cruises were made in 1966. The spring cruise assessed surf clam density and distribution in relation to bottom type and topography in the area from Montauk Point, Long Island, to Ocracoke Inlet, North Carolina. The fall cruise repeated stations established in 1965 between Montauk Point, Long Island, and Cape Hatteras, North Carolina. Only minor changes were found in the distribution or density of surf clams since the 1965 cruise.

A study to establish growth rates of young surf clams was completed in 1966. Marked and unmarked young clams in Chincoteague Inlet, Virginia, were observed from October, 1964, through March, 1967. The mean length of 1-year-old clams is 45 mm; 2-year-old, 69 mm and 3-year-old, 91 mm.

Surf clams in the major fishing area off New Jersey usually spawn twice a year, in summer and in fall, but spawned only once (late September) in 1965. Analysis of water temperature records from Barnegat Lightship indicated that the sum of daily temperatures above 0° C between spawnings may be more important to the spawning pattern than abrupt temperature changes.

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pp. 625–626

PECTORAL FIN LENGTH OF JUVENILE ALBACORE.—The striking difference between juvenile and adult albacore, *Thunnus alalunga* (Bonnaterre), in the relative length of the pectoral fin can be attributed to allometric growth. Asano (1964), who plotted the length of the pectoral fin against the body length of albacore, including data from Kawasaki (1960) and Yabe *et al.* (1958), indicated that the relative growth of the pectoral fin changed at about 35 cm fork length. He fitted a series of straight lines, presumably by eye, through the points. Gibbs and Collette (1967) discussed the relative length of the albacore's pectoral fin for fish between about 43–118 cm FL.

Because of (1) the importance of the pectoral fin in identifying adult albacore, (2) the difference in the relative pectoral fin length in adult and juvenile albacore, and (3) the predictive value of regressions, I determined a more precise relationship between the pectoral fin length and body

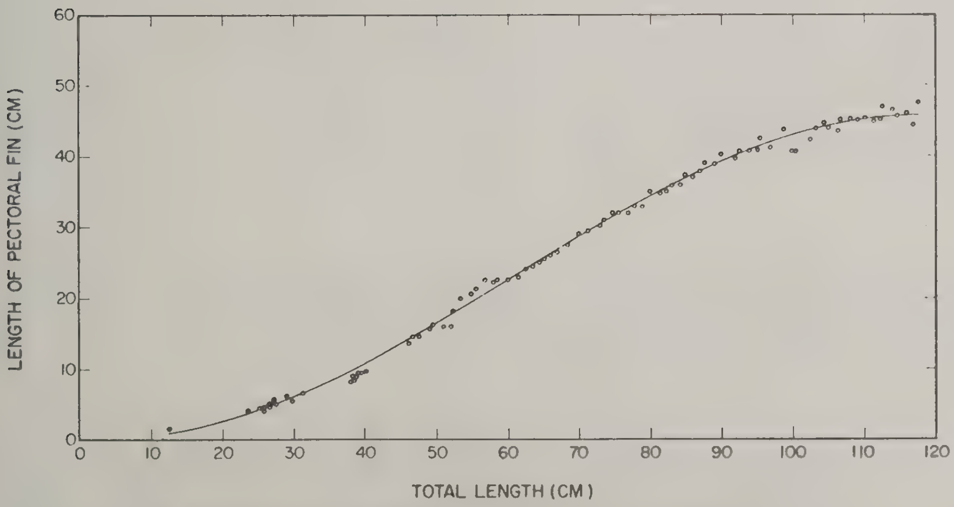

Fig. 1. Relation between length of pectoral fin and total length of albacore.

length than the series of straight lines of Asano.

In determining the relationship between pectoral fin length and body length, successively higher orders of polynomials were fitted to the data until an adequate fit was obtained. A third order polynomial provided an adequate fit to the data. The line is described by

$$\ell = 0.583162 - 0.125568L + 0.012139L^2 - 0.0000664636L^3,$$

where ℓ is pectoral fin length and L is total length (Fig. 1).

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HOWARD O. YOSHIDA, *U. S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii 96812.*

H.S.H. YUEN:

A PROGRESS REPORT ON THE USE OF A CONTINUOUS-TRANSMISSION, FREQUENCY-MODULATED SONAR IN FISHERY RESEARCH

1 INTRODUCTION 1
2 PRINCIPLES OF OPERATION 1
3 WORK IN PROGRESS 5
4 REFERENCES 8
5 FIGURES 9

1 INTRODUCTION

Fishery research, since its infancy at the turn of the century, has progressively involved more scientific disciplines. As a result of this expansion and advances in technology, methods in fishery research have not only increased but become much more sophisticated. The development of the capabilities of ships engaged in fishery research, as a natural consequence, has paralleled the growth and maturation of this science. As a recent example of this trend, the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, modified one of its ships, the CHARLES H. GILBERT, to accommodate the study of tuna behaviour by equipping it with facilities for underwater observations (Strasburg and Yuen, 1960). A newer ship, the TOWNSEND CROMWELL, was designed with underwater observation ports. A continuous-transmission, frequency-modulated (CTFM) sonar was installed on the TOWNSEND CROMWELL in 1966 to further its capabilities for research in tuna behaviour.

Possessing the ability to present high resolution information at a very rapid rate, the CTFM sonar is a new tool particularly suited for collecting data on the distribution and behaviour of tuna and other swift pelagic fishes. The first CTFM sonar applied to fishery research was used to classify fish by size through variations of the Doppler effect caused by variations in tail velocity (Hester, 1967). Although that sonar and the one on the TOWNSEND CROMWELL are based on the same principles, their characteristics are quite different, as the two systems were designed for different purposes. This paper describes the CTFM sonar and its auxiliary equipment installed on the TOWNSEND CROMWELL and summarizes part of the data collected to date. Although a description of this sonar was presented at the 12th Session of the Indo-Pacific Fisheries Council (Yuen, 1967), it is summarized here in consideration of the interest the members of this conference have in acoustic equipment for fishery research vessels.

2 PRINCIPLES OF OPERATION

The equipment of the entire system may be categorized functionally: the sonar equipment which collects the data, an interface unit connected to a tape recorder which records the data, an analog-to-digital converter, and a computer to retrieve and process the data. The recording equipment was recently installed and has not yet been used in the field.

The sonar unit is the model 505 of Straza Electronics.[1] As its name implies, the

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[1] Reference to the firm name in this publication does not imply endorsement of a commercial product.

Reprinted from Proceedings of the Second FAO Technical Conference on Fishery Research Craft, vol. 2, part 4.2/VI, 1968.

continuous-transmission, frequency-modulated sonar continuously transmits a signal that changes in frequency. The frequency modulation is in a sawtooth pattern (fig. 1). A returning echo from a target, e.g., a fish, will also have the same pattern of frequency change, but will lag the projected signal in time. The amount of lag depends upon the distance between the sonar and the target. The returning echo is compared with the signal being projected at the time of the return. The result is a difference in frequency (Δf) which is proportional to the magnitude of the lag and therefore proportional to target distance.

How the sonar functions may be gathered by tracing the path of the sonar signal is shown in fig. 2. A frequency-modulated oscillator generates a signal with a sawtooth pattern. The signal is amplified and relayed to the projecting transducer, which transmits it into the water. If there is a target, the signal is reflected back to a hydrophone, amplified in the pre-amplifier, and compared with the outgoing signal in the mixer. The resulting Δf is amplified and then displayed both audibly through a loudspeaker and, after being evaluated in a frequency analyzer, visually on a cathode ray tube (CRT).

The sonar operates in two frequency bands (table I): the "search" mode (52-32 kHz) covers ranges up to 1,600 m; the "classify" mode (290-260 kHz) provides high resolution at short ranges. Each mode requires its own projector, hydrophone, and mixer, but since other components are common to both, only one mode can be used at a time. In the search mode the resolution in bearing is 6° and in range 0.01 times the range scale selected. Bearing resolution in the classify mode is 0.6°. Range resolution is 0.0019 times the target distance.

The transducer assembly (fig. 3) consists of a separate projector and hydrophone for each mode. It can be trained horizontally through 360° and vertically from 0° (parallel to sea surface) to 90°. It is retracted into a sea chest when not in use. The sea chest has an outer diameter of 88 cm and extends 2.5 m into the ship. When lowered the upper transducer is 0.4 m beneath the hull and the lower, 1.5 m. This arrangement places them about 4 m beneath the sea surface.

The transducer assembly may be directed to scan automatically either horizontally or vertically. In the search mode the horizontal scanning may be over a sector of 12°, 45°, 90°, or 180°; otherwise, the size of the scanned sector is always 12°. A knob which controls tilt angle and a lever which controls horizontal rotation permit the positioning of the scanned sector.

TABLE I

Selected technical capacities of the search and classify modes of the CTFM sonar on the TOWNSEND CROMWELL

Characteristics	Search mode	Classify mode
Projected frequencies	52-32 kHz	290-260 kHz
Projector source levels (referenced to 1 μ bar at 1 m)	+100 db	+96 db
Beam shapes		
Projectors	Horizontal 38° Vertical 15°	Conical 15°
Hydrophones	Horizontal 6° Vertical 15°	(1) Horizontal 0.6° Vertical 15° (2) Horizontal 15° Vertical 0.6° (3) Conical 0.6°

The echoes are displayed on a 7-inch CRT. The display in the search mode is in the form of a plan position indication (PPI) and is scaled by choice to one of five available range scales: 100 m, 200 m, 400 m, 800 m, or 1,600 m. Also appearing on the CRT in the search mode is a cursor, a ring of light 5 mm in diameter. The position of the cursor on the CRT is controlled by the same lever which controls transducer rotation and is indicated in range and bearing by digital readouts. Thus, the position of a target may be obtained by placing the cursor on the target and reading the position of the cursor.

In the classify mode, the display is a "B scan", in which the limits of the display form a rectangle. The position in the centre of the rectangle is the cursor position. During automatic horizontal scanning the right and left borders of the display represent the right and left limits of the 12° sector being scanned. The top border represents a distance of 1.1 times the cursor range and the bottom border represents a distance 0.9 times the cursor range. During automatic vertical scanning the top and bottom borders represent the upper and lower limits of the scanned 12° sector. The left and right borders represent the distances mentioned previously. The position of the "B scan", like the cursor position, is controlled by the lever.

Other controls allow adjustment of the gain of the receiver and the audio display, correction of the cursor position to account for Doppler effects, and selection of active sonar or passive listening.

The Δf is analyzed by a frequency analyzer of 100 bandpass filters. The filters have a bandwidth of 50 Hz and cover a range of 500-5,500 Hz. The filters are scanned sequentially every 7 milli-seconds at a rate of a filter per 50 microseconds.

Recording operations are carried out by a 14-channel magnetic tape recorder (Sangamo model 3562). Two edge channels on the recorder add to 16 channels altogether. Sonar data recorded are: (1) signal levels from each filter of the frequency analyzer; (2) the synchronizing pulses which regulate the scanning of the frequency analyzer; (3) setting of receiver gain control; (4) operational information such as choice of search or classify mode, choice of range scale in the search mode, choice of beam shape in the classify mode, and choice of horizontal or vertical scanning; (5) transducer bearing; (6) transducer tilt; (7) cursor range; (8) cursor bearing; (9) Δf(fig. 4).

Information from sources other than the sonar and pertinent to the analyses of the sonar data are also recorded. The ship's gyrocompass (Sperry Mark 14 model 2a) provides signals on the course of the ship; gyroscopic sensors are the sources of pitch and roll information; an electromagnetic log system (Chesapeake Instrument model UL-100) measures and relays ship's speed; a time code generator-reader (Systron-Donner model HI-150) supplies the time of day to the nearest second; the interface unit generates a reference voltage. Miscellaneous information is recorded on one of the edge channels by voice.

The tape speed is 15 inches per second. A schedule of 2-second recording periods at 30-second intervals is initially being used. A timing device to automatically operate the recorder on this schedule or other schedules as the situation demands will be installed shortly.

The taped records are taken to the Statistical and Computing Center of the University of Hawaii and the data fed into an analog-to-digital converter (IBM 1827) tied into a computer (IBM 360/50). The converter is programmed to read the frequency analyzer channel 100 times in succession (once for each filter) on command of the recorded synchronizing pulses. This set of readings requires 5 milli-seconds and is repeated every 7 milli-seconds. The rest of the data channels are read during the 2 milli-second period following each reading of a set of data from the frequency analyzer. The digitized data are then sorted, reduced, and stored ready for analysis.

3 WORK IN PROGRESS

Much of the early work with the CTFM sonar has been aimed at evaluating the capabilities of the sonar in the field for the purpose of developing operational techniques and procedures (Yuen, 1967). One of the studies initiated at that time was a systematic sonar survey of three stations off the west coast of the island of Hawaii. The field work is completed but the data are still being analyzed. Another project under way is a study of the movements of skipjack tuna. The rest of this report will describe the procedures and the results to date.

Sonar surveys were made at three stations west of Hawaii (fig. 5). Stations 1 and 2 were close to the island over a steeply sloping bottom, the depth of which ranged from 900 to 1,800 m within the limits of the stations. Exposed to the effects of northeasterly trade winds which swept around the northern point of the island, station 1 differed from the well-protected station 2. Station 3 was over a depth of 4,100 m and was also subject to the effects of the trade winds.

The stations were surveyed five times. The order in which they were surveyed each time was randomized. Each survey was for 24 hours per station. The first three surveys were made during August 14-27, 1966. The last two were made during October 3-9 of the same year. The ship's track at each station described a rectangle 12 by 4 nautical miles. With the ship travelling at 4 knots the track was covered thrice each time a station was surveyed. Continuous salinity and temperature measurements to a depth of 500 m were obtained at the end of each 24-hour survey.

The sonar was operated to scan automatically ahead of the ship from beam to beam. The tilt angle was cycled to change from 80° to 0° in 10° increments. A change was made at the end of each beam-to-beam sweep. The range scale was alternated between 200 m and 400 m, the change taking place at the end of each cycle of tilt angle changes. The search pattern was interrupted when a target was detected. Upon detection of a target the sonar was trained on it so that data could be collected until it was out of range. Interruption of search rarely exceeded 4 minutes.

Station 2 had the highest number of targets in four of the five surveys (table II), and its 24-hour average of 96.6 targets was the highest. With a range of 12 to 121 targets for 24 hours, station 1 showed the greatest variability. The number of targets was considerably less in October than in August. The average number per survey in October was 63 percent of the August average.

The occurrence of targets in the August surveys showed a marked daily rhythm, but not those made in October.

TABLE II

Number of sonar targets in 24 hours

Survey no.		Station 1	Station 2	Station 3
(August)	1	30	83	65
	2	79	107	78
	3	121	118	90
(October)	4	37	76	58
	5	12	99	44
	Sum	279	483	335
	Mean	55.8	96.6	67.0

When the number of targets per hour, expressed as a percentage of the daily total, from all the August surveys was averaged and plotted against time (fig. 6), a major peak of occurrence between the hours of 0800 and 1300 and a minor peak at 1800 and 1900 were obvious. These peaks occurred consistently in the individual surveys. In contrast the surveys in October exhibited four peaks with little consistency between surveys.

The depth distribution of the targets was quite similar for all stations. The outstanding feature of the distribution (fig. 7) was the relatively large number of targets found in the top 10 m. The number at this level exceeded the number found at any other 10 m level by an order of magnitude. Apparent modes in the distribution were found at 20-30 m, 90-120 m, and possibly 160-170 m. Fig. 7 should be viewed with reserve as the numbers have not been weighted for the volume searched at various depths nor the effect of target strength. The somewhat involved analyses of these factors are under way.

In June 1967 the CTFM sonar was used to follow the vertical movements of skipjack and yellowfin tuna schools in the vicinity of the Hawaiian Islands. Schools were located either visually or with the sonar. Sonar contact with the school was then maintained as long as possible. During contact data were recorded at 30-second intervals.

Sonar contacts were made with 39 schools: 30 schools of skipjack tuna, 3 schools of yellowfin tuna, and 6 unidentified schools. The estimated size of the skipjack tuna ranged from 0.5 to 20 pounds. As is usual with skipjack tuna, all but two of the schools consisted of fish of uniform size. The yellowfin tuna schools were small and composed of individuals of an estimated 70 pounds.

Contact durations ranged from 20 seconds to 2 hours 35 minutes. Although sight was relied upon to maintain contact with surface schools on many occasions, contacts of 51 minutes and 1 hour 30 minutes with two skipjack schools, and 1 hour 54 minutes with a yellowfin school, were maintained exclusively by sonar.

Skipjack tuna appeared to change depth more freely than yellowfin tuna. The average rate of vertical movement for both species was 0.3 m/sec; rates ranged from 0 to 2.0 m/sec for yellowfin tuna and from 0 to 3.3 m/sec for skipjack tuna. The rate of movement towards the surface was the same as the rate of movement away from the surface for for both species.
The maximum depths attained by the skipjack tuna during any contact period (fig. 8) ranged from 4 to 195 m. The 195 m depth and one at 114 m, however, are subject to question as they were calculated from detection distances beyond those expected from the size of fish involved. The maximum depths attained by the yellowfin tuna schools were 38, 74, and 174 m.

Preliminary analyses indicate that the maximum depth reached by a skipjack tuna school may be correlated to the size of the fish in the school (Fig. 9). The correlation coefficient r is 0.739 (without the two questionable points mentioned earlier), significant beyond the 1-percent level. Although bathythermograph casts were made at the positions of most of the schools, the temperature profiles were so similar that the effect of temperature on vertical movements, if it exists, could not be determined.

Because surface skipjack schools are more readily located (i.e., by visual observation) than subsurface schools, much of the sonar work has been with schools originally at the surface. Skipjack tuna schools at the surface, however, present special problems in tracking. Surface echoes frequently remain stationary and fade away. The fading echoes are suspected to be from pockets of air which the skipjack bring into the water when they break the surface. Skipjack tuna in surface schools tend to move about independently of each other (perhaps because they are feeding), which makes them more difficult to track. Birds, which are usually associated with surface schools, are excellent reflectors of sonar signals when they are sitting on the water. This problem is considerably lessened once the sonar operator has learned to recognize echoes from birds.

In the summer of 1968 the apparent relation between size of skipjack tuna and depth limit will be investigated further. More effort will be made to determine the relation between the environment and the movements of skipjack tuna schools. The use of ultrasonic tags within the frequency range of the sonar will be attempted to extend the duration of sonar contact with the schools.

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Yuen, H.S.H., 1967 A continuous-transmission, frequency-modulated sonar for the study of pelagic fish. Proc.Indo-Pacif.Fish.Coun., 12 sect.2:258-270.

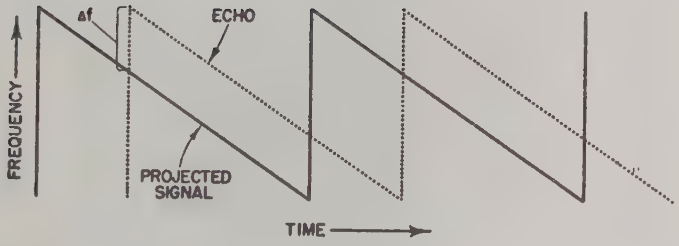
Δf
ECHO
FREQUENCY
PROJECTED SIGNAL
TIME

Fig. 1 Frequency difference (Δf) between projected signal and echo of CTFM sonar.

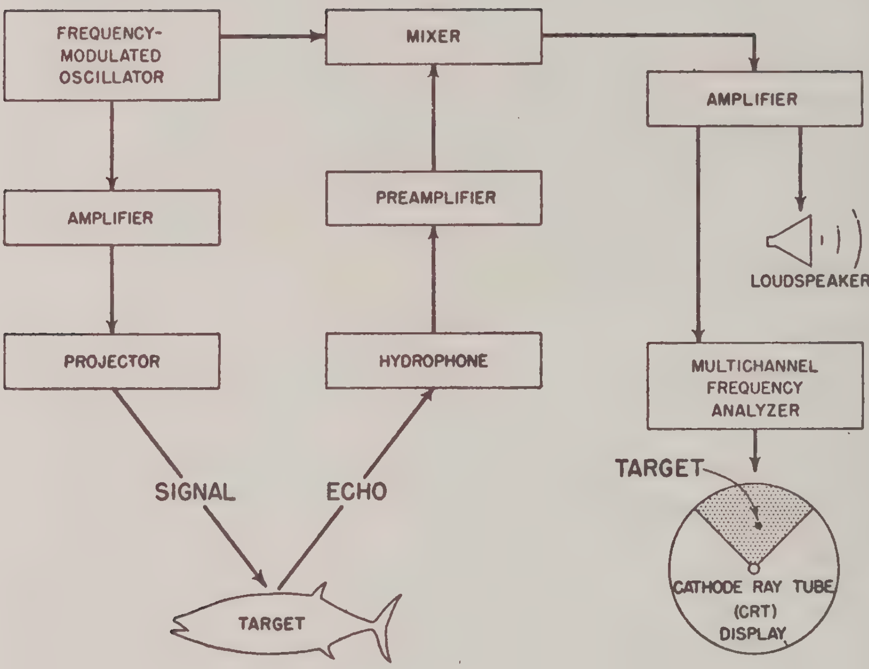
FREQUENCY-MODULATED OSCILLATOR
MIXER
AMPLIFIER
AMPLIFIER
PREAMPLIFIER
LOUDSPEAKER
PROJECTOR
HYDROPHONE
MULTICHANNEL FREQUENCY ANALYZER
SIGNAL
ECHO
TARGET
TARGET
CATHODE RAY TUBE (CRT) DISPLAY

Fig. 2 Simplified block diagram of CTFM sonar system.

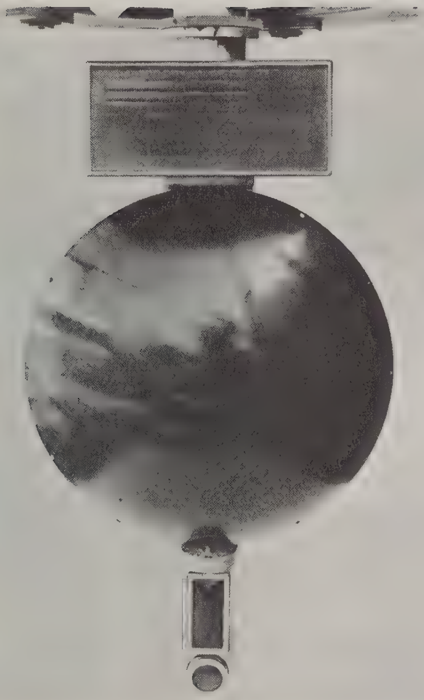

Fig. 3 Transducers of CTFM sonar on Townsend Cromwell. Top rectangle is search hydrophone; large circle is protective dome of classify hydrophone; bottom piece includes the search and classify projectors.

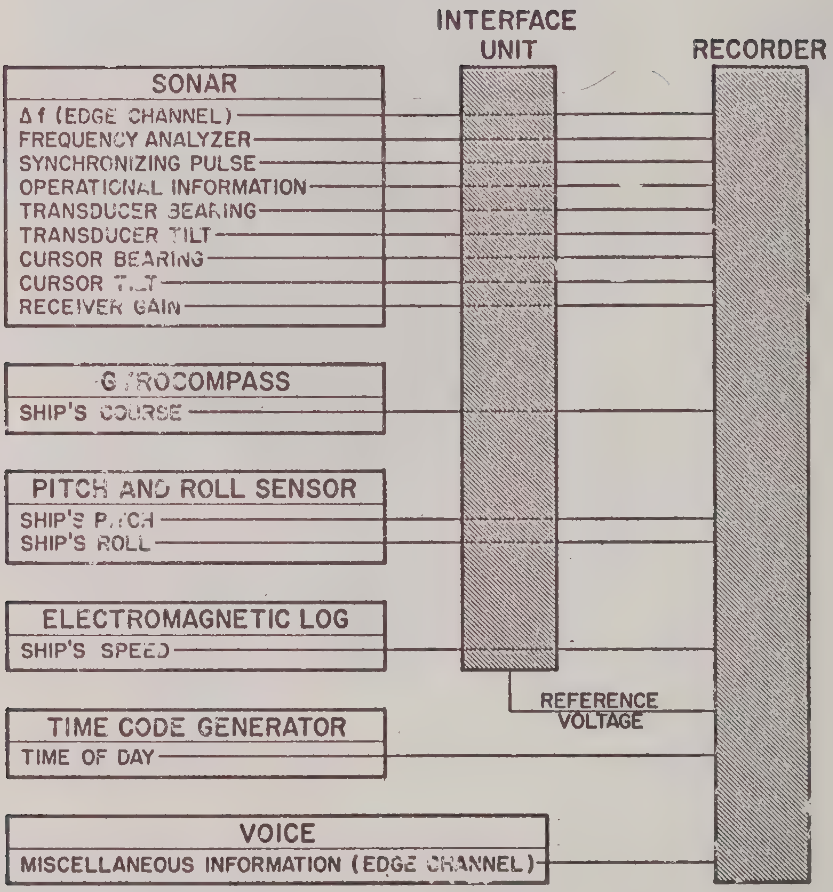
INTERFACE UNIT
RECORDER
SONAR
Δf (EDGE CHANNEL)
FREQUENCY ANALYZER
SYNCHRONIZING PULSE
OPERATIONAL INFORMATION
TRANSDUCER BEARING
TRANSDUCER TILT
CURSOR BEARING
CURSOR TILT
RECEIVER GAIN
GYROCOMPASS
SHIP'S COURSE
PITCH AND ROLL SENSOR
SHIP'S PITCH
SHIP'S ROLL
ELECTROMAGNETIC LOG
SHIP'S SPEED
REFERENCE VOLTAGE
TIME CODE GENERATOR
TIME OF DAY
VOICE
MISCELLANEOUS INFORMATION (EDGE CHANNEL)

Fig. 4 Diagram showing sources and paths of information to be recorded.

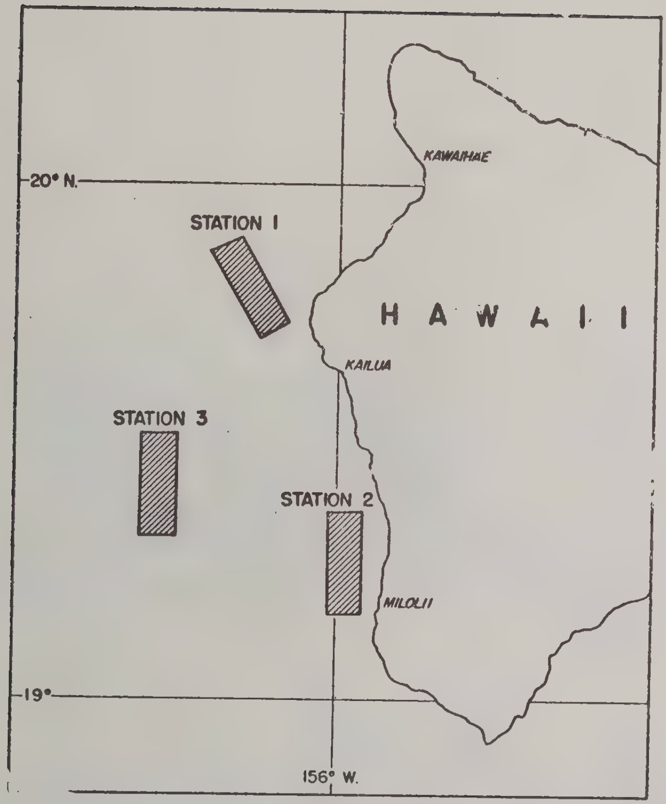
KAWAIHAE
20° N.
STATION 1
H A W A I I
KAILUA
STATION 3
STATION 2
MILOLII
19°
156° W.

Fig. 5 Positions of three sonar survey stations.

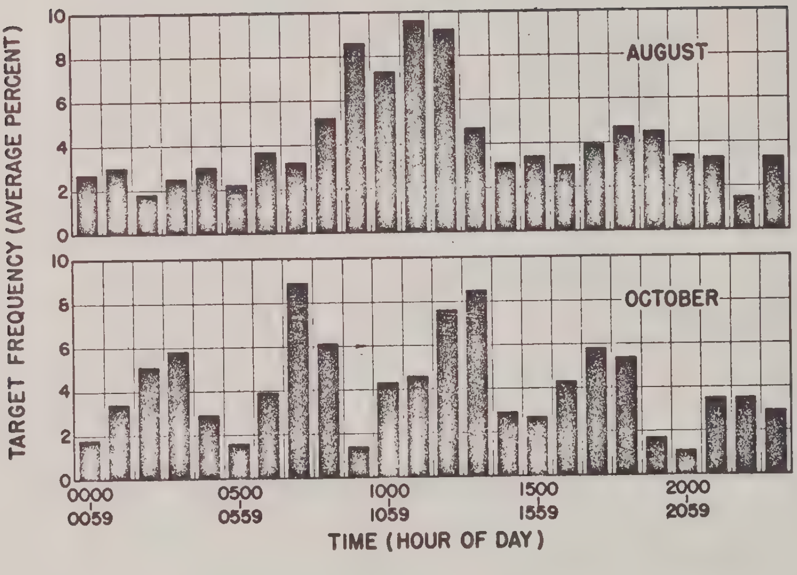

Fig. 6 Hourly distribution of sonar targets detected in August and October 1966.

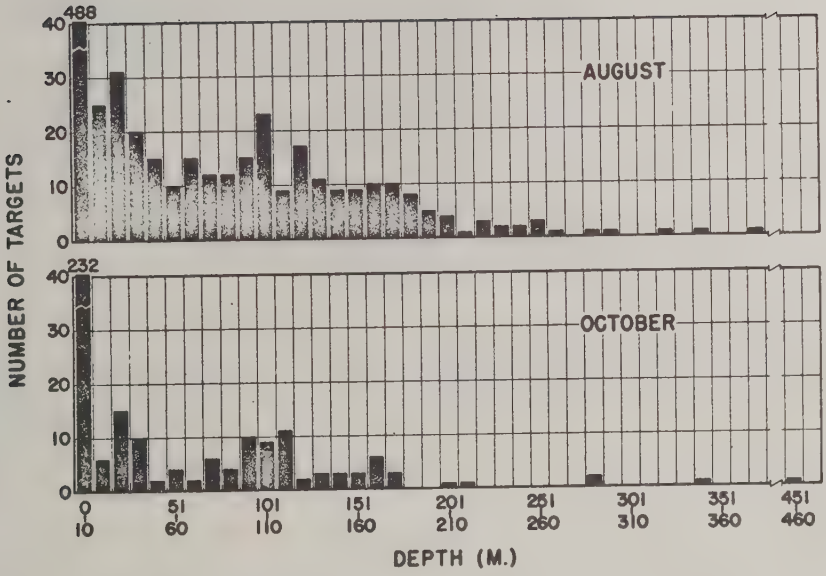

Fig. 7 Depth distribution of sonar targets detected in August and October 1966.

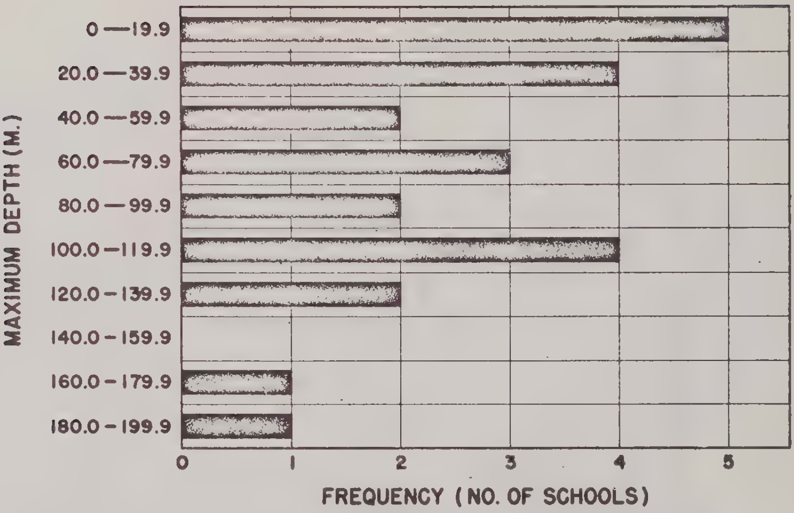

Fig. 8 Frequency distribution of maximum depths attained by skipjack tuna schools. .

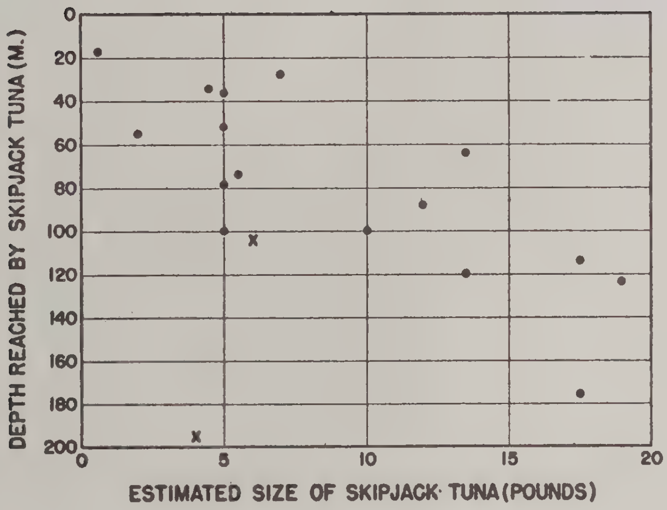

Fig. 9 Relation of size of skipjack tuna and maximum depth reached.

USE OF DORSAL CARINAL SPINES TO DIFFERENTIATE BETWEEN POSTLARVAE OF BROWN SHRIMP, *PENAEUS AZTECUS* IVES, AND WHITE SHRIMP, *P. SETIFERUS* (LINNAEUS)[1]

Gilbert Zamora and Lee Trent

Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas 77550

ABSTRACT

The presence of spines on the dorsal carina of the sixth abdominal segment of postlarval brown shrimp, *Penaeus aztecus* Ives, distinguished them with almost 100-percent reliability from postlarval white shrimp, *P. setiferus* (Linnaeus), in field collections from the tidal pass at Galveston, Texas.

INTRODUCTION

The presence of spines on the dorsal carina of the sixth abdominal segment of postlarval brown shrimp, *Penaeus aztecus* Ives, and pink shrimp, *P. duorarum* Burkenroad, and the absence of spines on the dorsal carina of postlarval white shrimp, *P. setiferus* (Linnaeus), were reported by Ringo and Zamora (MS). They concluded that this character was potentially useful in separating postlarvae of brown and pink (grooved) shrimp from white (nongrooved) shrimp. Their conclusions were based, however, on shrimp of known parentage reared in the laboratory.

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[1] Contribution No. 266, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

The objective of the present study was to determine the accuracy of the carinal spine character in separating postlarvae of brown and white shrimp taken in field collections.

METHODS

Postlarval shrimp were collected from the tidal pass at Galveston, Texas with a hand-drawn beam trawl and transferred alive to a holding tank in the laboratory. Each postlarva taken from the holding tank was placed in a depression plate, examined for the presence or absence of carinal spines, measured (total length—tip of rostrum to tip of telson), and placed in one of two tanks, depending on whether or not spines were present. No shrimp were discarded, and individual rearing tanks were used for each separated sample.

The postlarvae were fed brine shrimp (*Artemia* sp.) and reared to the juvenile stage (≥ 25 mm total length) by a technique described by Zein-Eldin (1963). After the shrimp became juveniles, they were taken from the tanks, preserved in 10-percent buffered formalin, and identified to confirm the earlier species separation based on the presence or absence of carinal spines.

ACCURACY OF IDENTIFICATION BASED ON THE CARINAL SPINE CHARACTER

The numbers of postlarval shrimp separated on the basis of the presence or absence of carinal spines, sampling dates, and mean total length of shrimp in each separated sample are shown in Table 1. The same table gives the numbers of postlarval shrimp reared to the juvenile stage for final identification. All

TABLE 1

Number and mean length of postlarvae separated according to the presence or absence of dorsal carinal spines and the number of juveniles identified as brown or white shrimp in relation to the initial identification based on the spine character

	Postlarvae in sample and mean total length				Identification of juveniles in relation to initial postlarval identification			
	Spines present		Spines absent		Spines present		Spines absent	
Sampling date	Number	mm	Number	mm	Brown	White	Brown	White
1967								
Feb. 14	150	12.3	0	..	135	0	0	0
Feb. 28	161	12.0	0	..	150	0	0	0
Mar. 13	150	12.0	0	..	118	0	0	0
Mar. 27	140	12.2	0	..	112	0	0	0
Apr. 13	150	12.6	0	..	106	0	0	0
May 10	142	10.4	0	..	106	0	0	0
May 26	26	10.5	100	6.9	18	0	0	93
June 27	74	10.5	99	7.0	57	1	0	88
July 11	125	10.7	20	7.0	93	0	0	13
Aug. 16	100	10.0	150	7.0	65	0	1	89
Sept. 14	79	11.0	168	8.0	8	0	0	136
Oct. 16	22	12.0	49	10.0	11	1	0	43
Total	1,319		586		979	2	1	462

juveniles were identified by the characters given by Burkenroad (1939) and Williams (1953).

The use of the carinal spine gave almost 100 percent accuracy in separating postlarvae of brown shrimp from postlarvae of white shrimp (Table 1). Of 979 postlarvae that had spines and survived to become juveniles, all but 2 were brown shrimp. Of 462 postlarvae without spines that survived to the juvenile stage, all but 1 were white shrimp.

The carinal spine character has proven useful in separating postlarvae of brown and white shrimp in the Galveston Bay area and in Louisiana (Woodrow Mock, Louisiana Wild Life and Fisheries Commission, Grand Isle, Louisiana; and Curt Rose, Francis T. Nicholls State College, Thibodaux, Louisiana, personal communication). The character is especially useful in parts of Texas, Louisiana, and other locations in the northern Gulf of Mexico because pink shrimp are rare in these areas (Baxter and Renfro 1967; Kutkuhn 1962).

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